COPULATORY BEHAVIOR OF *Rattus rattus*

By

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The copulatory behavior of a wild population of roof rats (Rattus rattus) was investigated in two experiments. In the first experiment the copulatory behavior of 12 pairs of laboratory-reared wild roof rats was observed on a total of 71 tests, each carried to a 30 minute satiety criterion. Females were brought into behavioral estrus with the aid of exogenous hormones. The basic motor patterns of copulation were described and the standard measures of copulatory behavior were taken. Categorizations of the behaviors accompanying copulation were also made on one test each for each male and each female of 11 pairs of animals. The occurrence and duration of bouts of ultrasonic vocalizations were also recorded on each of these 22 categorization tests.

With regard to most of the aspects of their copulatory behavior, roof rats appeared essentially identical to laboratory or Norway rats (Rattus norvegicus). Roof rats

were found to display a pattern of copulatory behavior characterized by no copulatory lock, no intravaginal thrusting, multiple ejaculations and usually multiple intromissions prior to ejaculation. Roof rats were also similar to Norway rats with regard to most of the quantitative measures of copulation, the behaviors accompanying copulation and patterns of ultrasonic vocalization. Both male and female roof rats were observed to emit ultrasonic vocalizations at 28 kHz during copulation.

In the second experiment the role of multiple ejaculations in the initiation of pregnancy was investigated. Sixteen young females were mated twice, once to males mating to only one ejaculation and once to males mating to a 30 minute satiety criterion. Eighty-seven percent of the females mated to satiety became pregnant while only 56% of the females mated to one ejaculation became pregnant. It was concluded that like Norway rats, roof rats may reach the maximal probabilities of pregnancy with only one ejaculation, although it appears that roof rats may require more intromissions than Norway rats to become progestational.

The results from these two experiments were compared to similar data from other muroid rodents and the results were discussed in terms of the adaptive significance of variations in copulatory behavior. Finally, the differences and similarities in copulatory behavior of roof rats and laboratory rats were discussed in terms of possible behavioral isolating mechanisms between the two species.

INTRODUCTION

The research reported in this dissertation provides the first quantitative description of the copulatory behavior of wild roof rats (Rattus rattus). Included in this description is an analysis of the behaviors accompanying copulation, including ultrasonic vocalizations. In addition there is an experimental analysis of the role of multiple ejaculations in the initiation of pregnancy in this species. To provide a rationale for this research and to review the appropriate background literature the introduction has been divided into several sections. The first section provides the rationale for studies of copulatory behavior and of adaptive significance. The latter sections review the relevant literature in these areas, provide some background information about roof rats and outline the research to be reported.

The Study of Copulatory Behavior

Mammalian copulatory behavior provides an excellent locus for comparative behavioral analysis. Among the reasons for this are the following. First, it has been found that the copulatory behavior of mammals is highly stereotyped within species but can show considerable variability between different species. Second, copulatory

behavior is of great biological significance, being near the heart of biological fitness. Finally, copulatory behavior can be studied in the laboratory making it an excellent preparation for experimental analysis.

The variability seen in patterns of copulation among mammals provides the very essence of comparative behavior analysis. If there were little variability in copulatory behavior, comparative analysis would be impossible. The fact that the variability in copulatory behavior occurs primarily between species rather than within suggests that patterns of copulatory behavior may be under significant genetic control and subject to evolutionary pressures. This in turn suggests that species differences in copulatory behavior may be due to different environmental pressures selecting for certain patterns over others. As pointed out by Dewsbury (1972b), comparative analyses of these species differences and the evolutionary pressures responsible for them may contribute significantly to our general understanding of the evolution of both behavior and of reproductive systems in general. The ways in which mammalian copulatory behavior can vary will be summarized below.

The reproductive success of a particular mammalian organism is in large part dependent upon its success in copulatory behavior. Except in cases of human intervention, organisms that do not engage in appropriate copulatory behavior do not leave offspring. The biological fitness

of an organism is expressed in terms of the relative numbers of viable, fertile offspring left by that individual, in sexually reproducing organisms. Efficient, successful copulatory behavior is absolutely essential in order to maximize reproductive success and hence, biological fitness. Successful copulatory behavior involves a number of factors. Mating must occur when there are maximal probabilities that viable, fertile offspring result. Similarly, the mating itself must not only transfer adequate numbers of sperm from male to female, but must also provide the necessary and sufficient stimulation to induce successful pregnancy. Studies by Adler (1969), Dewsbury and Estep (1975), and McGill (1970), have shown that the simple transfer of sperm is not sufficient to induce normal pregnancy in some mammalian females and that specific patterns of copulatory stimuli from the male may be necessary. Small variations in these normal patterns of behavior can disrupt normal reproduction and hence lower biological fitness (Adler, 1969; Adler & Zoloth, 1970). It is clear, therefore, that copulatory behavior is near the heart of the reproductive success of an individual.

For a number of reasons copulatory behavior is an excellent behavior pattern for laboratory study. It is first of all highly stereotyped in its appearance and can be reliably elicited under a variety of conditions. Few mammalian behavior patterns show such stability. In addition, the occurrence of copulatory behavior does not

depend upon prolonged training or extended practice among subjects. All of this means that the investigator can generate stable baselines in behavior both within and between subjects of a given population. Such stable baselines are ideal for experimental analyses and detailed comparisons across populations and species.

The Description of Copulatory Behavior

Comparative analysis begins with the basic description of the events to be compared. Before comparisons become meaningful, however, it is necessary to develop a system of classifying the behaviors observed. Dewsbury (1972b) has developed a taxonomy of mammalian copulatory behavior which suggests the ways in which copulatory behavior can vary and provides a framework for summarizing and comparing patterns of copulatory behavior.

As Dewsbury (1972b) points out, various aspects of the entire copulatory situation may vary from species to species. First, the antecedent conditions for copulation may differ. Some species, for example, breed seasonally while others breed the year round. The time of day, location of copulation and social context may also be significant and vary between species. Second, the nature of courtship or precopulatory behaviors may vary. Some species may have elaborate courtship behaviors while others do not. Third, the postures assumed during copulation may vary. Some species such as humans have ventral-to-ventral

copulation (Ford & Beach, 1951) while others, such as rats, have dorsal-ventral copulation (Beach & Jordan, 1956). Fourth, the behaviors accompanying copulation may vary. In some species such as laboratory rats, (i.e., domesticated Norway rats, Rattus norvegicus), copulation itself may account for less than one percent of the total time of a copulatory sequence (Dewsbury, 1967). The behaviors occurring during the rest of the time may vary considerably among species. Finally, the copulatory behavior itself may vary in a qualitative or quanitative fashion.

After careful review of the available data on copulatory behavior in mammals, Dewsbury (1972b) proposed that copulatory behavior may vary in four basic ways. First, there may or may not be a lock or physical tie between male and female during copulation. Second, intravaginal thrusting may or may not occur after the male has gained penetration. Third, multiple insertions without sperm transfer, may or may not be necessary prior to ejaculation. Finally, multiple ejaculations may or may not occur during the copulatory sequence. As there are two alternatives to each of these four attributes of copulatory behavior, there are 2^4 or 16 different patterns of behavior possible. Dewsbury has classified the copulatory behavior of laboratory rats for example, as pattern #13 because laboratory rats (Rattus norvegicus) show no copulatory lock, have no intravaginal thrusting, have multiple intromissions prior to ejaculation and have multiple ejaculations within a normal copulatory

sequence. House mice (Mus musculus) by contrast, have been assigned pattern #9 on the basis of the lack of a copulatory lock, and the presence of intravaginal thrusting, multiple intromissions and multiple ejaculations.

The various attributes of copulatory behavior can vary quantitatively as well as qualitatively. The frequencies and durations of copulatory events may vary as well as the latencies and intervals between events. Laboratory rats, Mongolian gerbils (Meriones unguiculatus), and rice rats (Oryzomys palustris), for example, all display pattern #13 copulatory behavior but show substantial variability with regard to the quantitative measures of copulation (Beach & Jordan, 1956; Davis, Estep & Dewsbury, 1974; Dewsbury, 1970). Any complete description of the copulatory behavior of a given species must include an account of the quantitative variations as well as the qualitative variations.

Descriptions of the copulatory behavior of mammals can be found scattered throughout the biological and behavioral literature. However, as Dewsbury (1972b) notes, most of these descriptions are inadequate for most comparative purposes. In recent years Dewsbury and his colleagues have been collecting systematic quantitative descriptions of the copulatory behavior of a variety of muroid rodents (See for example, Dewsbury, 1970; 1971; 1972a; 1973b; 1974a; 1974b; Estep, Lanier & Dewsbury, in press; Gray & Dewsbury, 1973). These studies provide the kind of complete descriptions

discussed above (including analyses of motor patterns, quantitative and qualitative variations in pattern and behaviors accompanying copulation) that are necessary to facilitate interspecific comparisons. Other good descriptions are to be found scattered among other groups of mammals such as primates (See Dewsbury, 1972b).

Among the behavioral patterns found to accompany copulation, one of the most interesting is the occurrence of ultrasonic vocalization. These high frequency vocalizations have been reported to occur in a variety of species and in a variety of social situations (Sewell, 1970). With regard to the ultrasonic vocalizations occurring during copulatory sequences the work of Barfield and Geyer (1972; 1975) on laboratory rats is most important. They have found that male laboratory rats have regular patterns of ultrasonic vocalization that follow most ejaculations. They have described and quantified this pattern in detail and have discussed its possible biological functions. Descriptions of such patterns in other species would provide added detail to the description of the behaviors accompanying copulation and perhaps allow some assessment of the functions of such behaviors in different species.

The Adaptive Significance of Variations in Copulatory Behavior

While the description of copulatory behavior is a worthwhile and necessary first step in the understanding of

mammalian copulatory patterns, it is not an end unto itself. Such descriptions achieve significance only when related to some meaningful question concerning copulatory behavior. One such question concerns the biological function or adaptive significance of variations in copulatory behavior. Students of animal behavior have often wondered why different species of mammals display such diversity in their copulatory behaviors. However, few systematic studies have been generated to investigate this question. Dewsbury (1972b) and his colleagues are attempting one such systematic investigation within a taxonomically restricted group of mammals - muroid rodents. By studying a behaviorally diverse but closely related group such as the muroids, probabilities of discovering the biological significance of differences in copulatory behavior are greatly enhanced. How then, might one investigate the adaptive significance of variations in copulatory behavior?

Methods in the Study of Adaptive Significance

Dewsbury (1973a) lists three methods for investigating questions of adaptive significance: The method of adaptive correlation, the behavior-genetic method and the experimental method. The first, the method of adaptive correlation, involves correlating variations in the behavior of interest with variations in other behaviors, morphology and ecological variables. By sampling a variety of organisms with different behaviors and looking for such correlations,

commonalities and consistent differences should become apparent that would suggest the functions of such differences and the environmental pressures responsible for them. A classic example of this method is presented by Cullen (1957) in the study of cliff nesting Kittiwakes. She was able to relate specific reproductive adaptations of these birds to their cliff nesting habits when comparisons were made to related non-cliff nesting gulls. The functions of these special adaptions to the nesting habitat became clear only when compared to other species who differed in their nesting habits.

The behavior-genetic method involves the use of inbred lines of animals and therefore is of restricted utility. This method involves comparing the behavior of F_1 hybrids with the behavior of the inbred lines that gave rise to them. By comparing the scores of the F_1s to those of the parents, conclusions can be drawn concerning the strength of the selective pressures operating on the parental types and therefore the adaptedness of the behavior. Bruell (1964, 1967) discusses the utility of this method in some detail. A recent example of this method is the work of Dewsbury (1975b). He has utilized this method to investigate the adaptive significance of variations in the copulatory behavior of laboratory rats.

The final method discussed by Dewsbury is the experimental method. By directly manipulating the behavior or the results of the behavior and looking for effects on

reproductive success or fitness, one can suggest possible adaptive functions for the behavior. A good example of this method concerns the egg shell removal behavior of gulls studied by Tinbergen (1963). Many gull species engage in egg shell removal behaviors soon after chicks are hatched. By systematically removing and replacing egg shells of various colors and looking at chick mortality, Tinbergen was able to show that egg shell removal helped prevent detection of the nest by predators and reduced chick mortality. The behavior was clearly adaptive and increased the reproductive success of those engaging in such behavior. Similar analyses have been carried out by Adler and his colleagues (See Adler, 1974 for a review), Dewsbury and Estep (1975) and Lanier, Estep and Dewsbury (in press) in an attempt to discover the adaptive significance of variations in copulatory behavior. The results of these analyses will be summarized below.

Each of the three methods discussed above has its own set of advantages and disadvantages. The methods differ with regard to the kinds of information they can generate and the requirements for their utilization in terms of subjects and procedures. It should be noted that the methods are not contradictory in nature but may, in fact, be used to complement each other to provide a more thorough analysis of the adaptive significance of a particular behavior.

For a number of reasons, the experimental method may be particularly attractive to those engaged in laboratory investigations of copulatory behavior. First, it does not necessarily require that a number of species be studied and compared directly. Second, investigations such as those of Adler, Dewsbury and Estep and others might be conducted along with a basic description of the copulatory behavior of a species thus allowing immediate access to information concerning the possible adaptive significance of the pattern described. Finally, experimental analyses of adaptive significance can provide data for a level of comparative analysis beyond simple description.

Variations in Copulatory Behavior and Reproductive Success

What, then, is the adaptive significance of variations in copulatory behavior? How might variations in copulatory behavior affect reproductive success and fitness? Adler (1969) and others have found that apparently small variations in male copulatory behavior can directly affect the female's reproductive physiology and thereby affect reproductive success. In a comprehensive review of the mammals, Adler (1974) notes that variations in male behavior can affect a female's reproductive physiology at many points in her reproductive life. Perhaps the most intensively studied of these phenomena concerns the effects of male behaviors on various aspects of the normal reproductive cycle of adult females.

As Adler notes (1974) the normal mammalian ovarian cycle has three sequential phases: 1) the follicular phase when ova and their follicles grow and mature, 2) the ovulatory phase when the mature follicle releases the egg and 3) the luteal phase when the ruptured follicle becomes a corpus luteum which secretes progesterone which aids in the maintenance of pregnancy. Conaway (1971) notes that there is considerable variability among mammalian species in the lengths of the various phases of the ovarian cycle, their occurrence and the kinds of stimuli necessary to elicit or modify them. In some species, for example, the ovulatory phase only occurs when the female receives copulatory stimulation. These animals are referred to as induced ovulators. Prairie voles (Microtus ochrogaster) and montane voles (Microtus montanus) are induced ovulators (Gray, Davis, Zerylnick & Dewsbury, 1974; Richmond & Conaway, 1969). In other species, such as laboratory rats, ovulation occurs spontaneously. Similarly, the luteal phase may be spontaneous, as in humans, or induced, as in laboratory rats. While it has been known for quite some time that copulatory behavior was instrumental in initiating some of these physiological changes, the exact nature of the stimuli remained obscure. A series of experiments by Adler and his colleagues was designed to analyze the effects of variations in male laboratory rat behavior on successful pregnancy in the female by affecting her reproductive physiology.

Male laboratory rats typically have a number of mounts and mounts with vaginal penetration, called intromissions, prior to ejaculation. An organized group of such mounts and intromissions, terminating in ejaculation is termed an ejaculatory series. Male laboratory rats normally display several such ejaculatory series prior to sexual satiation (that is, a period of 30 minutes with the same female without an intromission or ejaculation).

Wilson, Adler and Le Boeuf (1965) found a correlation between the amount of copulatory stimulation delivered by sexually vigorous males and the probability of pregnancy in the females receiving this stimulation. One group of females was allowed to mate undisturbed until the males attained their first ejaculation, usually after about nine intromissions. The other group was mated with males which only had three or fewer intromissions prior to their first ejaculation. Ninety percent of the females allowed a full complement of intromissions became pregnant while only 22% of the females receiving three or fewer intromissions became pregnant. Wilson et al. thus demonstrated that multiple intromissions prior to ejaculation (not just the ejaculation itself) were necessary to initiate normal pregnancy in young virgin female laboratory rats. Adler (1969) later replicated these results using a different strain of rats.

Apparently, the male's behavior functioned in two ways to induce normal pregnancy. First Adler (1969) found that

a sufficiently high number of preejaculatory intromissions was necessary for normal sperm transport. Those females having only one intromission prior to ejaculation had no sperm in their uteri 1-3 hours after copulation while those that had 2 or more intromissions had high numbers of sperm in their uteri. Chester and Zucker (1970) later extended these results and found that only 50% of the females receiving one ejaculation on the male's first insertion had sperm in their uteri 1/2 - 4 hours later. The biological importance of such rapid sperm transport was demonstrated by Adler (1968, 1969). He found that those females receiving high numbers of intromissions prior to ejaculation had normally developing embryos 3 days after copulation while those receiving low numbers of preejaculatory intromissions had unfertilized and degenerating ova in their fallopian tubes. Thus multiple intromissions were necessary for normal sperm transport and fertilization. It should also be noted that the ejaculatory reflex and the hard coagulated copulatory plug delivered by the male at ejaculation were also found to be necessary for normal sperm transport (Blandau, 1945).

The second way in which the male's behavior was found to influence the initiation of pregnancy in the female was through the induction of the luteal phase of the cycle. As noted earlier, the luteal phase is induced in laboratory rats and is essential for the maintenance of normal pregnancy in the female. The progesterone secreted by the corpus

luteum is essential for preparing the uterus to receive the fertilized embryo and allowing implantation. Adler (1969) showed that 100% of the females given a high number of intromissions showed a cessation of behavioral receptivity while only 18% of the females given three or fewer intromissions showed a cessation of behavioral receptivity. This implied a release of gestational hormones in response to the high levels of stimulation which in turn caused the cessation of behavioral receptivity. In a further elaboration of this work, Adler (1969) gave varying numbers of intromissions to females but did not allow them to receive an ejaculation. His data show that the proportion of females ceasing behavioral receptivity increased as a function of increased copulatory stimulation. Adler (1968) further showed an increased incidence of pregnancy among females inseminated following reduced numbers of intromissions if an injection of exogenous progesterone were given following copulation. Finally, Adler, Resko and Goy (1970) measured circulatory levels of plasma progestins directly in females given varying amounts of copulatory stimulation and found a direct correlation between the amount of copulatory stimulation and levels of progestin. All of these data confirm the importance of multiple intromissions in the induction of the luteal phase and the subsequent production of progestins, which is in turn essential for the maintenance of normal pregnancy. Although the mechanism is not yet fully understood, experimental

evidence reviewed in Adler (1974) suggests that the induction of the luteal phase occurs as a result of a neuroendocrine reflex which stimulates corpora lutea growth and thus the secretion of progestins.

All of the above evidence suggests that the frequency of intromissions is important in induction of normal pregnancy in laboratory rats. Work by Adler and Zoloth (1970) further suggests that the timing of copulatory events in laboratory rats may also be important. They found that if ejaculations were followed too closely by additional intromissions or by manual cervical stimulation, sperm transport and presumably, pregnancy could be disrupted. Thus the patterning of post-ejaculatory events is also important in induction of normal pregnancy.

The work of Adler and his coworkers shows that a single normal ejaculatory series provides the necessary and sufficient stimulation for induction of normal pregnancy. However, laboratory rats typically have multiple ejaculatory series. If one ejaculation normally provides all the stimulation necessary for normal pregnancy, what then is the biological function of multiple ejaculatory series? Recent work by Davis (1974) provides one possible answer. Davis found that while one ejaculatory series was indeed sufficient to induce normal pregnancy in young, virgin female laboratory rats, this was not the case in older multiparious females. Davis found that none of the older females receiving one complete ejaculatory series became

pregnant while 66% of those receiving 3 series and 92% of those receiving five series became pregnant. Moreover, those receiving five series had significantly more developing embryos in their uteri than those receiving only 3 series. Because none of the older females receiving just one series showed a cessation of regular estrous cycles, it was suggested that the reproductive failure of these females was due to inadequate induction of luteal function. Subsequent measurements of plasma progestins in older females receiving varying numbers of ejaculations supported this suggestion. It appears therefore, that multiple series delivered by a male could extend the reproductive life of aging females and increase the number of offspring produced, thus increasing the fitness of those males delivering multiple ejaculations.

Copulations beyond the first ejaculation also appear to be important in the induction of pregnancy in young females of other species. Dewsbury and Estep (1975) have demonstrated that only 5% of the cactus mice (Peromyscus eremicus) females given just one ejaculatory series become pregnant. Forty-seven percent and 60% respectively of the females allowed to mate to satiety and to satiety plus pairing overnight became pregnant. Thus, copulation beyond the first ejaculation in this species is necessary to maximize the probabilities of pregnancy. Work by Lanier et al. (in press), has shown a similar effect in Syrian golden hamsters (Mesocricetus auratus). In two experiments

they found that 20% and 40% respectively, of the females receiving just one copulatory series became pregnant. In both experiments 100% of the females mated to a 15 min satiety criterion became pregnant. They also demonstrated a direct relationship between the number of ejaculatory series received and the proportion of females becoming pregnant. They concluded that multiple ejaculations are essential in Syrian golden hamsters to maximize the probabilities of pregnancy.

It should be clear from this review of the literature that variations in male copulatory behavior can dramatically effect the reproductive physiology of the female, the induction of pregnancy and ultimately the fitness of organisms involved. Experimental investigations of the biological function of various aspects of the male's copulatory pattern have suggested possible functions for various aspects of the patterns such as multiple intromissions and multiple ejaculations. In addition species differences have been found in the function of similar aspects of the behavior. Laboratory rats and Syrian golden hamsters have multiple intromissions and multiple ejaculations; however, multiple ejaculations maximize the probability of pregnancy in young female hamsters while they do not in young laboratory rats. As mentioned previously, experimental investigations of the biological function of patterns of copulation carried out in conjunction with basic descriptive analyses provide an added level of

analysis to comparative investigations of copulatory behavior. They also facilitate the study of the adaptive significance of variations in copulatory behavior and contribute to our general understanding of the evolution of behavior and reproductive systems. Few such descriptions and experimental analyses exist, however, even for species of muroid rodents. Such a detailed description of the copulatory behavior and an experimental analysis of the biological functions of the behavior seems particularly warranted for one species of muroid rodent - the roof rat (Rattus rattus). Roof rats are closely related to the common laboratory rat and are very common, living in close association with man. However, very little is known of their behavior including their copulatory behavior.

The Natural History of Roof Rats

According to Simpson (1945), the roof rat or black rat (Rattus rattus L.) is a member of the order Rodentia, superfamily Muroidea, family Muridae and subfamily Murinae. Simpson recognizes 68 different genera within the Murinae, one of which is the genus Rattus. According to Ellerman (1941), there are over 554 forms in the genus, many of which are subspecies. Walker (1964) notes that this makes the genus Rattus the largest genus of all mammals. Most of the 284 distinct species recognized by Ellerman are tropical in distribution and are found chiefly in southeast Asia and Africa (Walker, 1964). Two species have gained world wide

distribution: the Norway rat, Rattus norvegicus, and the roof rat, Rattus rattus. Norway rats tend to be a more temperate species and are thought to have originated in the area around the Caspian Sea, whereas roof rats are considered to be a more tropical species originating in Indo-Asia (Robinson, 1965).

According to Walker, Robinson and others, both roof rats and Norway rats gained their global distributions through their associations with men. Roof rats supposedly were first brought to Europe during the crusades by Europeans on their way back from the Middle East. Roof rats brought with them the plagues which ravaged Europe during the 12th, 13th and 14th centuries. The Norway rat supposedly did not get to Europe until approximately the 16th century. In northern climates the newly introduced Norway rat quickly displaced the smaller, less vicious roof rat. In more tropical climates the displacement of roof rats by Norway rats has been much slower. According to Walker (1964) roof rats reached North America with the first explorers, while Norway rats did not reach North America until the 18th Century.

Roof rats and Norway rats are very similar morphologically but can be distinguished by several reliable keys. According to Hall and Kelson (1959) Norway rats are larger in body size than roof rats. Norway rats have 12 teats while roof rats have only 10. Roof rats have tails longer than their entire bodies while Norway rats have tails equal to or shorter than their body lengths.

Roof rats and Norway rats often exist as commensals of man, living in barns, grain storage areas and human habitations. Roof rats tend to be arboreal, nesting in the roofs of houses and barns, while Norway rats tend to nest in burrows or in protected nest sites on the ground. According to Telle (1966) and Ewer (1971) roof rats form complex social groups with a linear male hierarchy or dominant male type of social organization. Both Telle and Ewer report that group territories are actively defended against intruders. Barnett (1963), Ewer (1971) and Telle (1966) provide some information on other aspects of the behavior of this species such as foraging, aggression, parental care, maintenance activities and other social interactions. Barnett and Telle also discuss interspecific interactions between roof rats and Norway rats. According to Barnett (1963) roof rats and Norway rats do not hybridize in the laboratory or the field.

The Present Research

Ewer (1971) has observed the copulatory behavior of both captive and free ranging roof rats. She describes their behavior as conforming "...in general with what has been described by Barnett in Rattus norvegicus...[p.155]". Her description suggests that roof rats have a pattern characterized by multiple intromissions prior to ejaculation, no lock and probably multiple ejaculations prior to sexual satiety. This is indeed similar to the pattern shown by

Norway rats. While Ewer provides data on the events preceding copulation, postures and motor patterns assumed during copulation and a rough description of the copulatory pattern itself, much remains to be done to provide a detailed quantitative description of the copulatory behavior of this species. If the maximal information is to be gained from interspecific comparisons the copulatory pattern should be described in as much detail as possible. Without this added detail, conclusions about the adaptive significance of variations in copulatory behavior must remain tenuous and preliminary.

The research reported here consists of two experiments. The first provides a quantitative description of the copulatory behavior of roof rats. The second provides an analysis of the stimulation essential for initiation of successful pregnancy in this species. In addition to providing data that will facilitate interspecific comparisons and aid in our understanding of the adaptive significance of variations in patterns of copulation, these data might also provide some insight into possible behavioral isolating mechanisms between roof rats and Norway rats. As noted earlier the two species are occasionally sympatric, at times living in the same building, but never hybridizing. It is possible that one of the mechanisms preventing hybridization involves differences between the species in their copulatory behavior. If the differences were substantial enough, they might prevent the induction of

pregnancy when heterospecifics did happen to mate thus preventing successful hybridization.

EXPERIMENT 1

While detailed descriptions of copulatory behavior exist for a variety of muroid rodents including laboratory rats (Dewsbury, 1972b), no such detailed quantitative description exists for the common roof rat. This experiment was designed to provide such a description. Provided are an analysis of the basic motor patterns, a qualitative and quantitative description of the pattern of copulation, and a description of the behaviors accompanying copulation including ultrasonic vocalizations. Such detail should facilitate interspecific comparisons and provide a framework for experimental analyses of the adaptive significance of various aspects of the copulatory behavior of this species.

Materials and Methods

Subjects

All of the subjects of Experiments 1 and 2 were the first generation laboratory reared offspring of wild trapped animals. The parents of these subjects were 11 males and 8 females all live-trapped as adults at the University of Florida Poultry Farm, southwest of the main campus of the University of Florida. Several of these original specimens were positively identified as Rattus rattus L. after close

morphological examination by Dr. Steven Humphrey of the Florida State Museum.

The subjects for Experiment 1 were 12 male and 12 female laboratory reared offspring of these wild trapped animals. All the subjects were weaned at 30 days of age and housed in isolation in Wahman suspension cages measuring 18 cm x 17.5 cm x 24.5 cm. All animals received Purina Lab Chow and water ad lib. The colony was housed in an air conditioned room maintained at approximately 21° C. A reversed light-dark cycle of 16 hr light, 8 hr dark was enforced throughout the experiment with light onset occurring at 1800 hr daily. One 25 watt red light bulb illuminated the room at all times.

Apparatus

Animals were tested in clear plastic cages measuring 38 cm x 20 cm x 48.5 cm covered with stainless steel cage tops made of 2 mm diameter rods. San-i-Cel brand litter material covered the bottom of the cages and served as a substratum for testing. Behavioral events were recorded on a 20 channel Easterline-Angus event recorder and by hand with written descriptions when necessary. Ultrasonic vocalizations were detected with the aid of a Holgate Mark V ultrasonic receiver and a Telequipment Model S54A Oscilloscope. The oscilloscope was calibrated at 50 μsec/cm and 0.5 volts/cm. The ultrasonic receiver was calibrated with the aid of a frequency generator and was found to be accurate within ± 5 kHz in a range from 20 kHz to 100 kHz.

The ultrasonic receiver is a superheterodyne instrument that transduced the ultrasonic input into an audible output. This output was monitored directly with the use of headphones and on occasion the audible output was also fed into the oscilloscope and visual representations of the signal were observed.

Procedures

All of the males used in this experiment had been pretested for copulatory behavior at least once prior to the start of formal testing and proved to be reliable copulators. Pretesting consisted of pairing a male with a female in natural estrus and allowing him to mate uninterrupted for at least one hr. Males had not been allowed to explore the apparatus prior to pretesting. Females were not pretested for copulatory behavior prior to formal testing but all had been permitted to explore the test apparatus on at least one occasion of 20-30 min. All of the animals were between 130 and 180 days of age at the start of the experiment and between 210 and 260 days of age at the time of their final test.

Animals were tested in the colony room approximately 3 hrs after the beginning of the dark phase of the diurnal cycle. During the experiment four 25 watt red light bulbs illuminated the testing cages. Males were introduced into the cages 5 to 10 min before the start of testing and allowed to habituate to the situation.

Tests were started with the introduction of the female into the testing cage. Males were given 30 min from the

start of the test to initiate copulation. On tests where the male did not achieve an intromission within this time period, the test was terminated and scored as a "negative". On tests where the male did initiate copulation, the test was allowed to continue until 30 min had elapsed since the male achieved his last intromission or ejaculation. At this time the test was terminated and scored as a "positive". Each male was tested with the same female at two wk intervals until each pair had achieved six positive tests or had received four consecutive negative tests.

On the fifth and sixth positive tests for each pair a categorization was made of the behaviors accompanying copulation, and the occurrence of ultrasonic vocalizations in the 22-33 kHz frequency range was noted. On those tests where ultrasonic vocalizations were to be observed, the Holgate ultrasonic receiver was utilized, tuned to 28 kHz and the microphone was placed in the center of the food tray of the cage top.

All females were brought into behavioral estrus with intramuscular injections of 0.1 mg estradiol benzoate followed by 1.0 mg of progesterone given approximately 75 hrs and 5-6 hrs before testing, respectively.

Behavioral Measures

Pretesting had indicated that the copulatory pattern of roof rats was essentially the same as that of Norway rats. That is copulations were found to be organized into groups or series of mounts, mounts with vaginal penetration

(intromissions) and intromissions terminating in ejaculation (ejaculations). Each such organized series of copulatory behaviors usually ended with the occurrence of an ejaculation. Males have a number of such ejaculatory series before reaching sexual satiety. Accordingly, the standard measures of copulation for this species were adopted from those developed by Beach and Jordan (1956) for laboratory rats. These standard measures of copulation were:

ML - Mount latency. The time from the start of testing until the first mount with pelvic thrusting (with or without intromission).

IL - Intromission latency. The time from the start of testing until the first vaginal intromission by the male.

MF - Mount frequency. The number of mounts with pelvic thrusting but without intromission within an ejaculatory series.

IF - Intromission frequency. The number of intromissions within an ejaculatory series.

EL - Ejaculation latency. The time from the first intromissions of a series to the ejaculation of the series.

MIII - Mean interintromission interval. The mean interval separating the intromissions of a series. This is calculated by dividing EL by IF.

PEI - Postejaculatory interval. The time from the ejaculation of one series until the resumption of copulation as indicated by the first intromission of the next series.

It should be noted that the measures IF, EL and MIII are not completely independent of each other for a given ejaculatory series (EL = IF x MIII).

On those tests where ultrasonic vocalizations were to be observed, several measures of vocalizations were taken. The postejaculatory ultrasonic vocalizations of roof rats were found to be similar in pattern to those of Norway rats and therefore the parameters of postejaculatory vocalizations developed by Barfield and Geyer (1975) were utilized for roof rats. These measures were:

VL - Vocalizations latency. The time from the ejaculation until the beginning of the ultrasonic vocalizations.

VT - Vocalization termination. The time from the ejaculation until the end of the ultrasonic vocalizations.

In addition two derived measures were taken:

PEI-VT - An estimate of the time spent in ultrasonic vocalization. Calculated by subtracting the VT for a given copulatory series from the PEI in which it occurred.

VT/PEI - The proportion of the PEI spent in ultrasonic vocalization. Calculated by dividing the VT for a given series by the PEI in which it occurred.

After preliminary observations of the copulatory behavior of roof rats, a system was developed for the categorization of the behaviors accompanying copulation into several mutually exclusive categories. The occurrence and duration of each of these categories of behavior were

recorded on an Esterline-Angus event recorder and later decoded to generate a profile of the behaviors occurring during the various phases of the copulatory sequence. Using this system the behaviors accompanying copulation were categorized on the fifth positive test for each male and on the sixth positive test for each female. The categorization was initiated at the start of the test and terminated at the end of the 30 min satiety criterion. The behavioral categories were adapted from those of Dewsbury (1967; 1970; 1971; 1972a; 1973b; 1974a; 1974b) and are listed below. All behaviors are common to both males and females unless otherwise noted.

Mount (Males Only) - Mounting, intromitting or ejaculating by males.

Lordosis (Females only) - the posture taken by females when males mount. It involves a stance in which the female plants her feet firmly, straightens her hind legs and lifts her head forming an inverted arch in her back.

Chase (Males only) - Following or chasing the female orienting towards her at all times and usually culminating in a mount of the female.

Run From Male (Females only) - Involves the female's darting away from the male or running from a pursuing male. Simultaneous ear wiggling and tail rattling behaviors may also occur.

Sniff - Involves an approach or orientation toward the partner in which the animal appears to sniff the body of the partner.

Upright Defense - Occurs when the animal stands upright on its hind legs orienting the ventrum towards the partner. Sometimes involves pushing or slashing of the partner with the forepaws and/or audible vocalizations.

Genital Groom Self - Scratching, licking or manipulation of the animal's own genital area.

General Groom Self - Scratching, licking or manipulation of the animal's own body with the exception of the genital area.

Genital Groom Partner - Scratching, licking or manipulation of the partner's genital region.

General Groom Partner - Scratching, licking or manipulation of the partner's body with the exception of the genital region.

Groomed - A sitting posture adopted by an animal while being groomed by its partner. Ears are usually back and eyes are closed.

Climb - Climbing or hanging upside down on the cage top of the testing cage.

Pull Female (Males Only) - Slashing at or pulling on a female which is climbing or hanging on the cage top.

Feet on Walls - A posture in which the animal stands upright and leans against the sides of the cage with its forepaws.

Dig - Digging or pushing the substratum with the paws.

Locomotor-Explore - Walking movements sometimes accompanied by nosing of the substratum, walls or cage top,

mouthing or manipulation of the substratum or feces, and upright postures other than those listed elsewhere.

Sit - Adoption of a sitting posture by the animals involving little movement other than slight mouth and head movements.

Lie - Lying down. Self explanatory.

Results and Discussion

Basic Motor Patterns of Copulation

The basic motor patterns of copulation of roof rats were found to be almost identical to those of laboratory rats. Male roof rats mounted females several times prior to ejaculation. The male typically palpated the female's sides vigorously while making numerous rapid shallow pelvic thrusts. On some of these mounts the male gained vaginal penetration (intromission), characterized by a deep pelvic thrust followed by a rapid dismount; on other mounts the male dismounted without achieving intromission (termed mounts). Usually after several mounts and intromissions the male mounted, achieved intromission and ejaculated. The ejaculatory intromission was characterized by a much deeper pelvic thrust and a much slower dismount. The ejaculation was always followed by a period of sexual inactivity known as the postejaculatory interval (PEI). An organized chain of copulatory events culminating in an ejaculation (and including the following PEI) is known as an ejaculatory series. Male roof rats were found to achieve an average of 4.3 such ejaculatory series before reaching sexual satiety.

On three of the 302 ejaculatory series observed, three different males were observed to ejaculate on a single insertion, that is with no intromissions preceding the ejaculation. This pattern, although rare in roof rats, has never been observed in normal Norway rats. It is possible therefore that there is a fundamental difference between the two species with regard to this ability to ejaculate on a single insertion.

In a very strict sense roof rats are categorized as pattern #15 in Dewsbury's taxonomy of copulatory behavior (Dewsbury, 1972b) because they show no copulatory lock, no intravaginal thrusting, ejaculations can be achieved on a single insertion and because they typically attain multiple ejaculations. In that the phenomena of ejaculation on a single insertion was observed so rarely in roof rats, it might also be reasonable to classify roof rats as pattern # 13 animals. This pattern characterizes species such as Norway rats (Beach & Jordan, 1956), Syrian golden hamsters (Beach & Rabedeau, 1959), and Mongolian gerbils (Kuehn & Zucker, 1968) which have no lock, no intravaginal thrusting, multiple ejaculations and multiple intromissions always preceding ejaculation. The final resolution of this problem of classification awaits further data on other populations of roof rats. If the phenomenon of ejaculation on a single insertion proves to be very rare, then it would probably be more reasonable to classify roof rats as pattern #13.

Ewer's (1971) description of the copulatory behavior of a laboratory colony of roof rats and of a free-living population indicates that the animals she observed also displayed pattern #13 copulatory behavior. It is clear from her description of the behavior of the laboratory colony that the animals she observed had multiple intromissions and probably multiple ejaculations. No mention is made of the presence of a lock or of intravaginal thrusting. She also notes that while complete "sequences" of copulatory behavior were not observed in the free-living population "All stages were, however, seen a number of times on different occasions" [p. 156].

When mounted by a male, the female roof rats demonstrated a lordotic posture similar to that displayed by female laboratory rats. The lordotic posture was characterized by an extension of the hind legs and elevation of the head accompanied by a spinal flexure resulting in an inverted arch in the female's back. The tail was deflected laterally.

Prior to mounting, receptive females often displayed a series of behaviors including rapid ear wiggling, tail rattling and approaches to the male followed by rapid darting away and stopping several cm away. These behaviors were observed on every test in which the females were judged behaviorally receptive and were not observed in the few tests where the females were not behaviorally receptive. Females were judged behaviorally receptive solely on the basis of their responses to mounting by males: a behaviorally

receptive female adopted a lordotic posture in response to male mounting. It is of interest to note that Ewer (1971) observed the patterns of darting and tail rattling in free ranging wild Rattus rattus females during copulatory sequences. Ewer makes no mention of the pattern of ear wiggling observed in the present population of animals. Darting and ear wiggling have been reported numerous times for receptive female laboratory rats (Beach, 1942; 1943; 1956) but tail rattling has never been reported for this species.

Quantitative Measures of Copulatory Behavior

Quantitative data for the copulatory behavior of roof rats were collected on 71 tests from twelve pairs of animals. Each pair was to receive six tests each carried to a 30 minute satiety criterion; however one male died prior to his last test.

Table 1 presents the means and standard errors of the mean for the standard measures of copulatory behavior for the first three and the last three ejaculatory series. Standard errors were computed using a formula derived by Marks (1947). This formula was developed for those situations in which there are unequal numbers of tests for different subjects. As can be seen from Table 1, it took male roof rats an average of approximately 1.5 min to achieve their first mount and a little over two minutes to achieve their first intromission from the start of the test.

Table 1

Means and Standard Errors of the Standard Measures of Copulatory Behavior For the First 3 Series and Last 3 Series

Behavioral Measure	Series					
	1	2	3	N-2	N-1	N
ML[a]	98.5 ± 18.6					
IL[a]	146.3 ± 28.0					
EF	4.3 ± 0.4					
MF	5.1 ± 1.2	4.3 ± 2.0	3.6 ± 0.9	3.5 ± 0.9	3.6 ± 1.0	5.7 ± 2.3
IF	7.6 ± 0.7	2.8 ± 0.3	3.0 ± 0.2	4.4 ± 0.2	3.8 ± 0.3	3.3 ± 0.3
EL[a]	563.4 ± 118.5	170.8 ± 39.1	166.5 ± 28.1	226.1 ± 39.1	262.2 ± 86.5	340.4 ± 62.3
MIII[a]	70.3 ± 9.3	66.3 ± 14.5	69.6 ± 13.3	50.0 ± 7.6	52.5 ± 7.6	112.4 ± 22.4
PEI[a]	269.2 ± 15.5	308.5 ± 19.4	371.5 ± 27.5	345.6 ± 17.0	453.2 ± 32.0	----------

[a] Time measures in seconds

Once started, roof rats typically attained a mean of 4.3 ejaculations before reaching sexual satiety. Sexual satiety was attained between series on 46 of 71 tests or 64.8% of the time. This is to say, satiety was reached after the completion of an ejaculation and without the animal initiating another series, on 64.8% of the tests. On 35.2% of the tests, males initiated but did not complete an ejaculatory series before reaching sexual satiety. During their first copulatory series, male roof rats had a mean of 5.1 mounts and a mean of 7.6 intromissions prior to ejaculation. The mean interval between intromissions was found to be a little over one min while the mean ejaculation latency was somewhat over nine min in length. The mean postejaculatory interval following the first series lasted approximately four min.

Analyses of variance were performed for all eight of the standard measures of copulatory behavior to assess the effects of repeated testing on these measures. Those measures that occurred more than once per test (i.e. MF, IF, EL, MIII and PEI) were subjected to different analyses than those that did not (ML, IL, EF) in order to assess any changes that might occur across series as well as across tests.

Male roof rats were found to be remarkably variable in the number of ejaculations that they might attain on any given test. Males were found to have as many as eight ejaculations or as few as one ejaculation prior to reaching

sexual satiety. This variability in the number of series made analysis of data from all series for all tests on all subjects impossible. Therefore, only those animals having three or more series on their first four tests were included in the statistical analysis. Eight pairs of animals met this criterion and it is on the data from these animals that the following statistical analyses were performed.

The results of these analyses of variance are summarized in Table 2. Complete ANOVA tables for each measure appear in Appendix A. One way analyses of variance for repeated measures were performed on the measures ML, IL and EF to assess the effects of repeated testing on these measures. As the results in Table 2 show, there were no significant test effects for any of these measures. It can therefore be concluded that no significant changes occurred with regard to these measures over the first four tests.

For the measures MF, IF, EL, MIII and PEI, two way analyses of variance for repeated measures were performed. The results of these analyses also appear in Table 2. On no measure was a significant test effect found. Significant changes across series were noted for the measures IF, EL and PEI but not for the measures MIII and MF. None of the tests by series interactions proved to be significant.

The Newman-Keuls method (Winer, 1974) was applied to the measures IF, EL and PEI to determine which series were

Table 2

Results of Analyses of Variance of Eight Measures of Copulatory Behavior

Behavioral Measure	Source	df	F	p
ML	tests	3,21	2.30	NS[a]
IL	tests	3,21	1.33	NS
EF	tests	3,21	0.96	NS
MF	tests	3,21	1.45	NS
	series	2,56	1.42	NS
	tests x series	6,56	0.73	NS
IF	tests	3,21	1.32	NS
	series	2,56	58.40	<.001
	tests x series	6,56	0.87	NS
EL	tests	3,21	0.19	NS
	series	2,56	30.08	<.001
	tests x series	6,56	0.64	NS
MIII	tests	3,21	0.21	NS
	series	2,56	2.46	NS
	tests x series	6,56	0.76	NS
PEI	tests	3,21	1.81	NS
	series	2,56	68.42	<.001
	tests x series	6,56	1.11	NS

[a] NS = Not significant

Table 3

Results of Newman-Keuls Analysis for Three Measures of Copulatory Behavior

Behavioral Measure	Series	Mean and Standard Error	Comparison	r	q_r	
IF	1	6.8 ± 0.4	1 vs 2	3	13.95	*
	2	2.9 ± 0.2	1 vs 3	2	12.40	*
	3	3.3 ± 0.2	2 vs 3	2	1.55	
EL[a]	1	406.9 ± 45.6	1 vs 2	3	10.42	*
	2	84.9 ± 6.5	1 vs 3	2	8.16	*
	3	154.8 ± 33.4	2 vs 3	2	2.26	
PEI[a]	1	249.6 ± 10.6	1 vs 2	2	0.60	
	2	283.1 ± 11.6	1 vs 3	3	16.34	*
	3	341.6 ± 15.6	2 vs 3	2	10.41	*

Note. df = 56 for all comparisons

[a] Time Measures in Seconds

* $p < .01$

significantly different from the others for each of these measures. The results of these analyses appear in Table 3. For IF and EL it was found that the means for the first series were significantly larger than the means for the second series and the third series. Means for series two were not significantly different from means for series three for either measure. For PEI, the mean for the third series was significantly greater than the means for the first and significantly greater than the means for the second. The mean PEI of series one was not significantly different from the mean PEI of series two.

It can be concluded from these results that no significant changes as a function of test occurred over the first four tests in any of the eight standard measures of copulatory behavior. Significant changes across the first three series can be seen only for the measures IF, EL and PEI. For the measures IF and EL significant decreases are seen from first to later series. For PEI the third series shows a significant increase over the first two.

The changes in the standard measures of copulatory behavior across series are of considerable interest. Several studies have dealt with the changes in copulatory behavior of laboratory rats as sexual satiety is approached (Beach & Jordan, 1956; Dewsbury, 1968; Karen & Barfield, 1975). This research was generated primarily by an interest in the nature of the underlying mechanisms responsible for such changes. It is therefore of some theoretical interest to

compare the changes in the copulatory behavior of laboratory rats and roof rats as satiety is approached. The statistical procedures performed previously do not allow for an adequate analysis of changes in copulatory behavior as satiety is approached because only the first three series were analyzed and on many tests the animals completed more than three copulatory series. The means and standard errors presented in Table 1 provide some indication of changes that occurred in various measures as male roof rats approached sexual satiety. With this method of data presentation means and standard errors were determined for the first three series for all subjects. Then the means and standard errors were calculated for the last complete copulatory series (or Nth series) regardless of whether it was the eighth or the first series. In a similar fashion the next to last series (N-1) and the second from the last series (N-2) were computed. This system does not accurately portray the changes across series for those tests where considerably more or fewer than six series are needed to reach satiety. For example, on a test where only two series were completed before satiety was reached, data from those two series were represented twice as the first and second series respectively and as the N-1 and N series, respectively. For a test where eight series were completed the first three series were represented in series one, two and three, respectively and the last three series were represented in the series labeled N-2, N-1 and N. The middle two series

would not be represented at all. Given the considerable variability shown in ejaculation frequency across tests for roof rats another method of data presentation was employed for the analysis of changes in behavior as satiety was approached. This method was originally developed by Larsson (1956) and later refined by Karen and Barfield (1975) for use with laboratory rats. The essence of the system involves plotting the changes in behavior across series as a function of the number of completed series obtained prior to sexual satiety. Means were calculated for all tests from all animals that had only two series prior to satiety, all tests where the animals had only three series prior to satiety and so on until curves were generated for all tests where two, three, four, five and six ejaculations occurred prior to satiety. No curves were generated for those tests in which one, seven or eight ejaculations were obtained, there being too few such tests to construct meaningful curves. Finally, these separate curves were plotted on a variable axis, thus allowing direct comparison of all initial and terminal points for each measure regardless of the number of ejaculations received. Figures 1 through 4 present these data for the measures IF, EL, MIII and PEI, respectively.

Figure 1 reveals that there was a clear decline in IF from first to later series. In addition, those tests where three, four, five and six ejaculations occurred prior to satiety showed a small but consistent rise in IF during the terminal series.

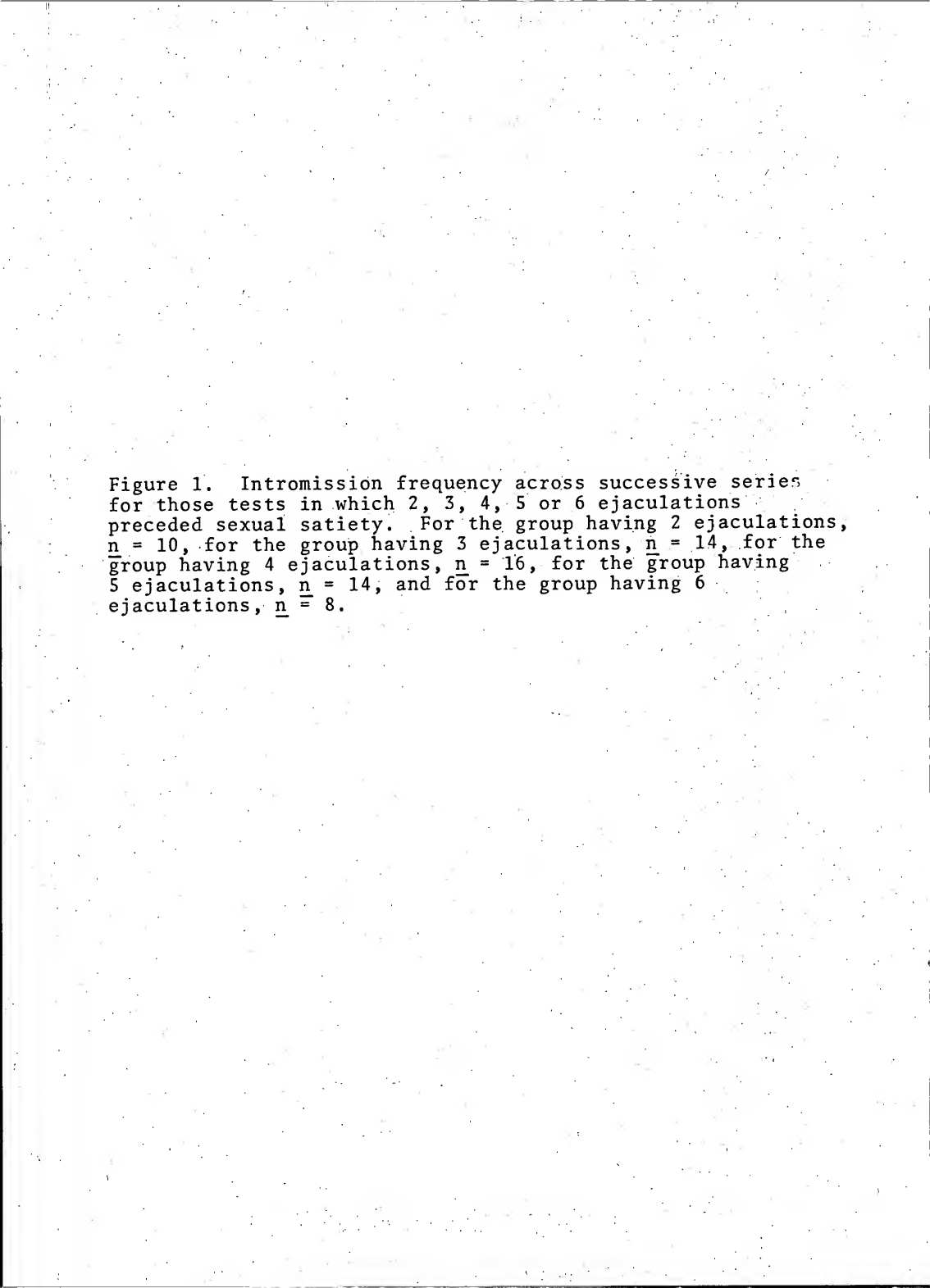


Figure 1. Intromission frequency across successive series for those tests in which 2, 3, 4, 5 or 6 ejaculations preceded sexual satiety. For the group having 2 ejaculations, $\underline{n}$ = 10, for the group having 3 ejaculations, $\underline{n}$ = 14, for the group having 4 ejaculations, $\underline{n}$ = 16, for the group having 5 ejaculations, $\underline{n}$ = 14, and for the group having 6 ejaculations, $\underline{n}$ = 8.

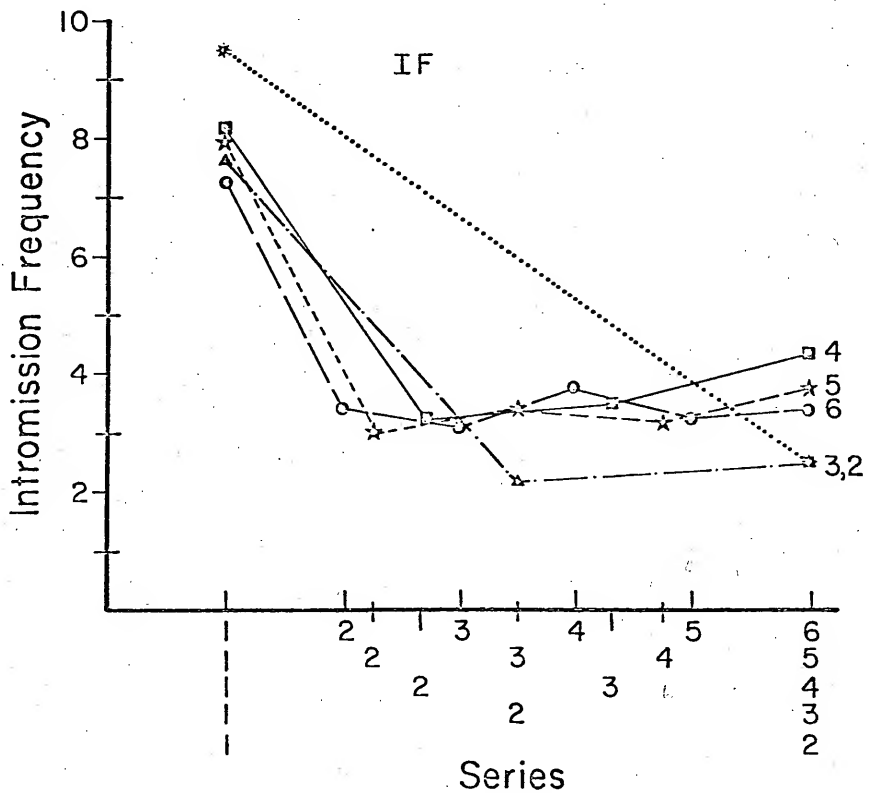

Intromission Frequency
10
8
6
4
2
IF
4
5
6
3,2
2
3
4
5
6
Series

Figure 2. Ejaculation latency across successive series for those tests in which 2, 3, 4, 5 or 6 ejaculations preceded sexual satiety. For the group having 2 ejaculations, $\underline{n}$ = 10, for the group having 3 ejaculations, $\underline{n}$ = 14, for the group having 4 ejaculations, $\underline{n}$ = 16, for the group having 5 ejaculations, $\underline{n}$ = 14, and for the group having 6 ejaculations, $\underline{n}$ = 8.

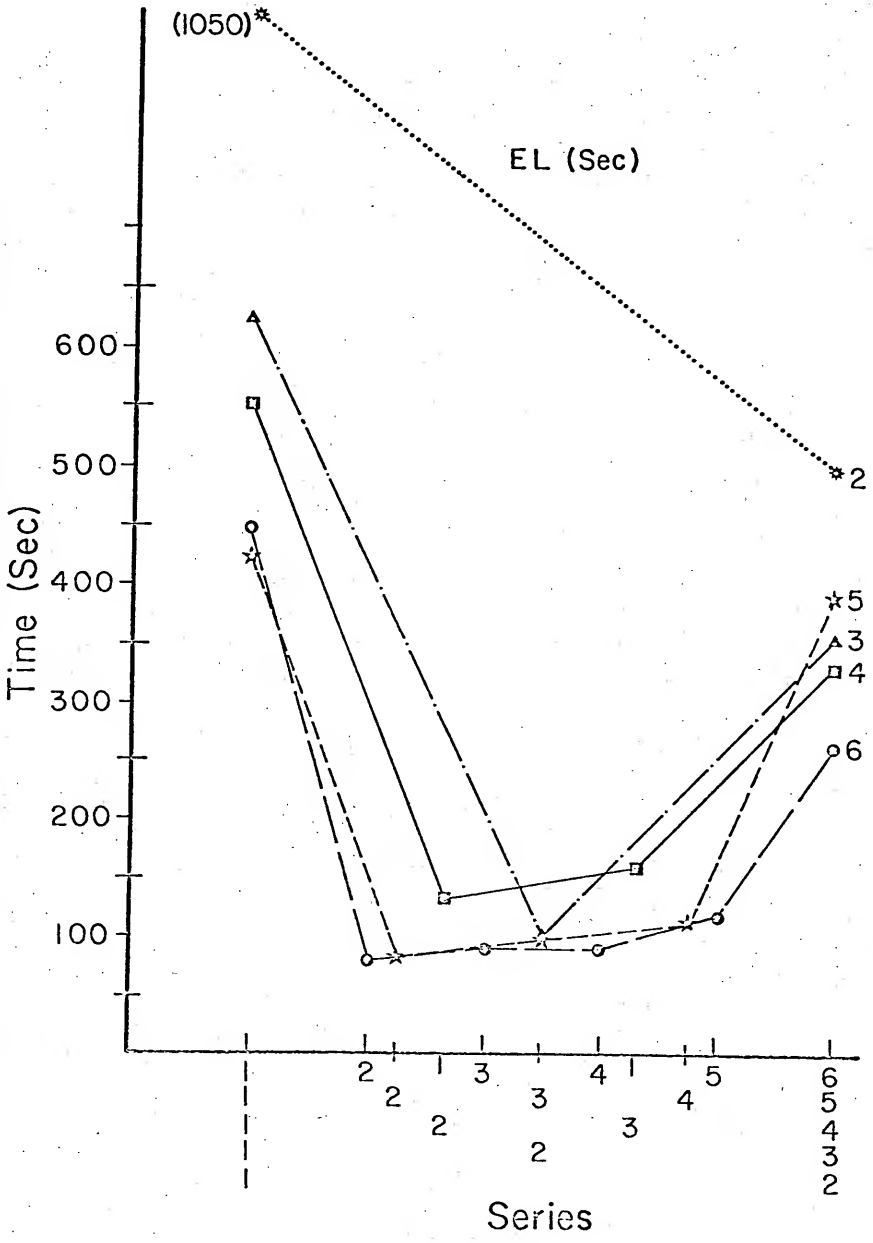

(1050)
EL (Sec)
600
500
400
300
200
100
Time (Sec)
2
5
3
4
6
2 2 3 4 5 6
2 3 4 5 4
2 3 4 3
2 3 2
2
Series

Figure 3. Mean interintromission interval across successive series for those tests in which 2, 3, 4, 5 or 6 ejaculations preceded sexual satiety. For the group having 2 ejaculations $\underline{n}$ = 10, for the group having 3 ejaculations, $\underline{n}$ = 14, for the group having 4 ejaculations, $\underline{n}$ = 16, for the group having 5 ejaculations, $\underline{n}$ = 14, and for the group having 6 ejaculations, $\underline{n}$ = 8.

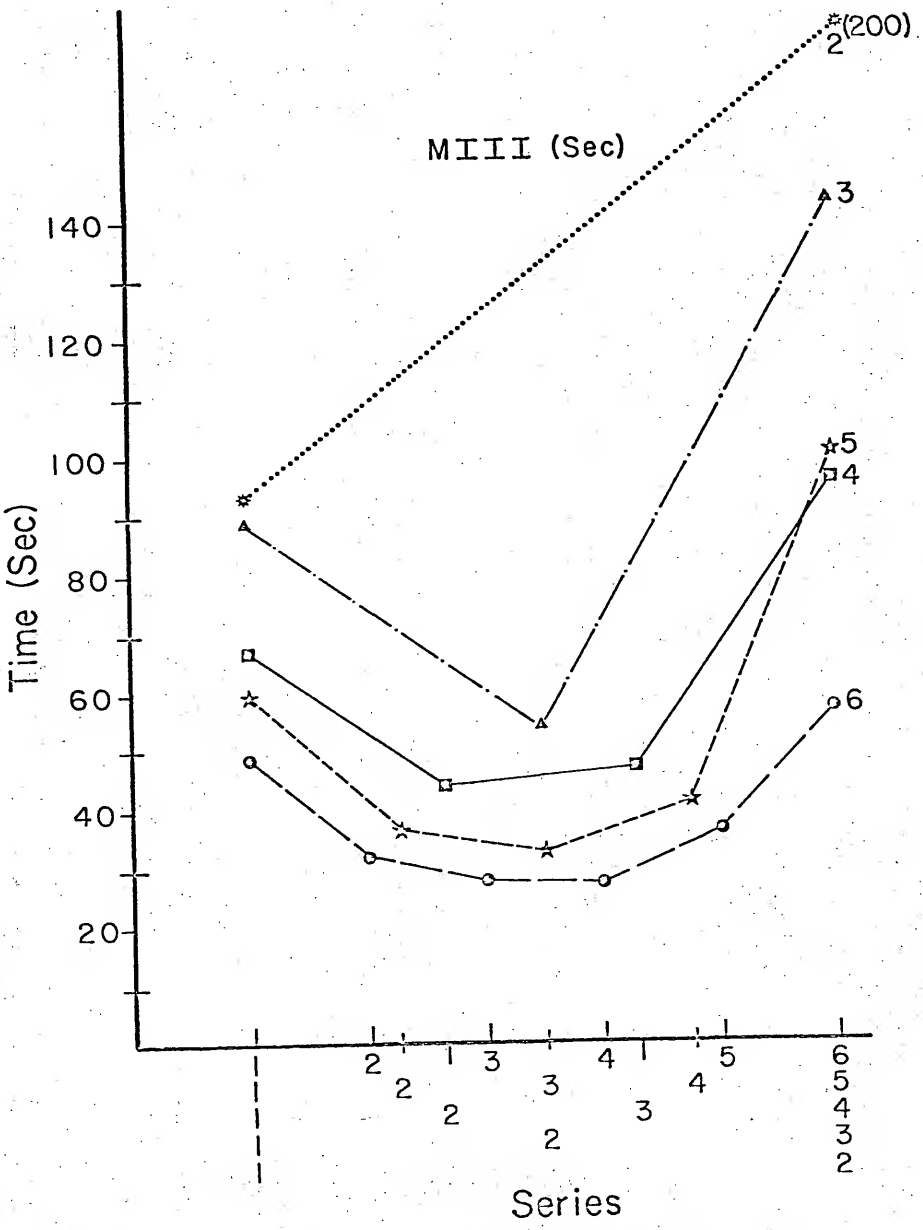
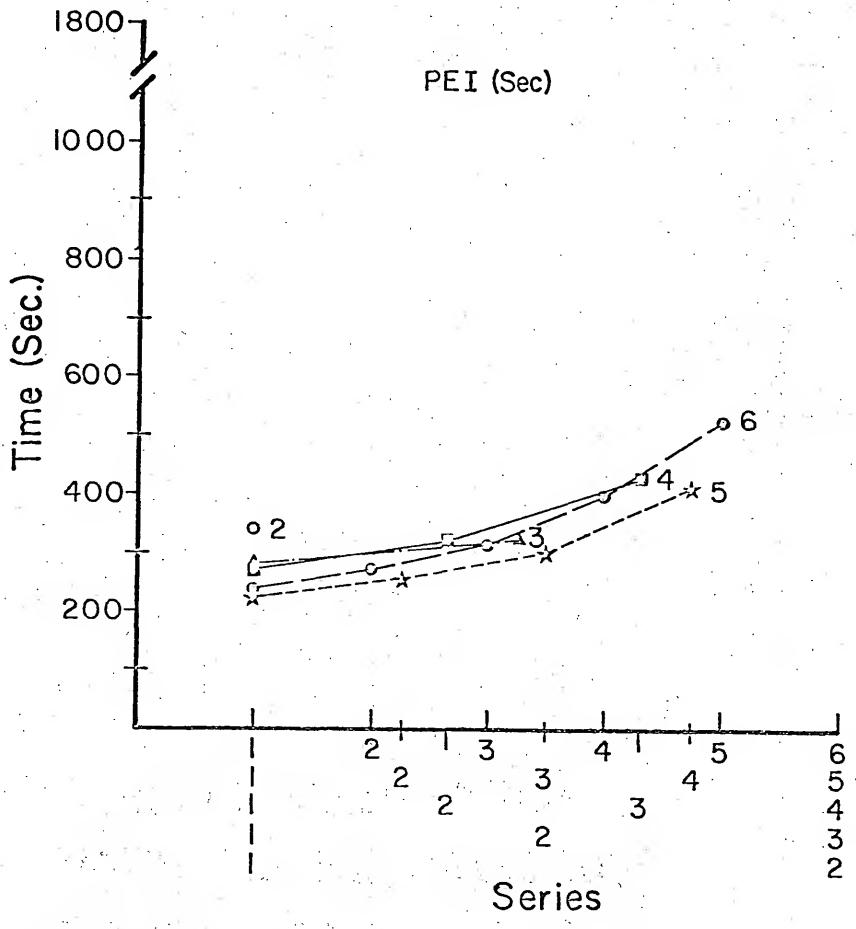

MIII (Sec)
Time (Sec)
140
120
100
80
60
40
20
2(200)
3
5
4
6
Series

Figure 4. Postejaculatory interval across successive series for those tests in which 2, 3, 4, 5 or 6 ejaculations preceded sexual satiety. For the group having 2 ejaculations $\underline{n}$ = 10, for the group having 3 ejaculations, $\underline{n}$ = 14, for the group having 4 ejaculations, $\underline{n}$ = 16, for the group having 5 ejaculations, $\underline{n}$ = 14, and for the group having 6 ejaculations, $\underline{n}$ = 8.


PEI (Sec)
Time (Sec.)
1800
1000
800
600
400
200
2
3
4
5
6
Series

The graphs for EL in Figure 2 and for MIII in Figure 3 reveal very similar U-shaped functions for most tests. For the tests in which three, four, five and six ejaculations occurred the EL showed a decline from first to middle series and then an increase in the terminal series. For those tests in which only two ejaculations took place, EL declined from first to last series. The measure MIII is seen in Figure 3 to have declined from first to middle series and then increased rapidly in the later series for those tests in which three, four, five and six ejaculations occurred. For those tests in which only two ejaculations occurred the MIII increased from first to last series.

While the measures IF, EL and MIII appeared to display more or less U-shaped functions the measure PEI seen in Figure 4 appeared to have an entirely different function. As satiety was approached, the PEI tended to increase across successive series, rather than decrease and then increase.

It had been noted earlier that with regard to the basic motor patterns of copulation, roof rats were found to be very similar to laboratory rats. Roof rats also appear to be quite similar to laboratory rats with regard to the quantitative measures of copulatory behavior. Table 4 compares the present quantitative data for roof rats with those from three different strains of laboratory rats in two different studies by Dewsbury (1968; 1975b). The measures compared are ML, IL, MF, IF, EL, MIII and PEI from the first

Table 4

Comparisons of the Standard Measures of Copulatory Behavior Between Roof Rats (Rattus rattus) and 3 Strains of Laboratory Rats (Rattus norvegicus)

Behavioral Measure	Roof Rats[a]	Laboratory Rats[b]		
		LEW[c]	F344[c]	Long-Evans[d]
ML	98.5 ± 18.6	85	239	-------
IL	146.3 ± 28.0	191	359	-------
EF	4.3 ± 0.4	------	-----	7.4
MF	5.1 ± 1.2	13.9	7.4	6.7
IF	7.6 ± 0.7	11.9	9.8	10.8
EL	563.4 ± 118.5	1057	607	687
MIII	70.3 ± 9.3	95	65	62.6
PEI	269.2 ± 15.5	533	314	372

[a] Data expressed as means and standard errors

[b] Data expressed as means

[c] Data from Dewsbury, 1975

[d] Data from Dewsbury, 1968

copulatory series and EF for those strains tested to satiety. These data were chosen for comparison because they were collected in the same laboratory in which the roof rat data were collected and because procedures were much the same for all three studies. The ML and IL for the LEW strain were very close to those observed for roof rats while the other measures differed considerably between the two species. For the measures MF and MIII both the F344 strain and the Long-Evans strain appear close to the range of scores for roof rats. For the measures EL and PEI the F344 strain more closely approximates the scores shown by roof rats. The intromission frequency in the first series appears somewhat lower for roof rats than any of the three laboratory rat strains presented here.

The ejaculation frequency also appears somewhat lower for roof rats than for the Long-Evans strain. Comparisons of EF's from three other studies show that laboratory rats tested in different laboratories with varying amounts of prior sexual experience do show some variability in this measure. Beach and Jordan (1956) tested both albino and hooded strains and found the average EF to be 6.2 and 6.4 in two different experiments. Dewsbury tested Long-Evans rats with varying amounts of prior sexual experience and found the EF to vary between 5.5 and 7.6. Males with very little sexual experience had lower EF's than those who had considerable experience. These scores are still somewhat higher however, than the EF of 4.3 observed for roof rats.

As the data in Table 4 and the above mentioned data for EF illustrate, there is some variability in the copulatory behavior of laboratory rats tested in different laboratories. Some of this variability is due, no doubt, to differences in housing, maintenance and testing procedures of the animals, prior sexual experience and other environmental variables. Some of the variability is also due to genetic differences between strains of laboratory rats. Several studies have shown there to be quantitative differences in the copulatory behavior of different strains of laboratory rats (Dewsbury, 1975 b; McLean, Dupeire & Elder, 1972; Whalen, 1961). This variability within laboratory rats makes it difficult to assess possible species differences between roof rats and laboratory rats with regard to the quantitative measures of copulation. To adequately compare the behavior of these two species it would be necessary to rear and test representatives of both species under identical conditions. Given the strain differences in behavior it would also be necessary to sample a wide range of domesticated and wild populations of Rattus norvegicus and to also sample a range of wild populations of Rattus rattus. Under these conditions it would be possible to draw firm conclusions about species differences in the quantitative aspects of copulatory behavior.

Despite the limitations of comparing the behavior of different species from different experiments, several points can be made from the data presented in Table 4. In that the

mean ML and MIII for roof rats fall within the range of means presented for laboratory rats, it is probable that the two species do not differ with regard to these measures. The measures MF, IF and EL show considerable individual variability for the roof rats tests as can be seen by the high standard errors. In fact 24% of the IF's, 26% of the MF's and 30% of the EL's collected for roof rats fall within the range of scores presented for laboratory rats. These data suggest that with regard to these three measures roof rats and laboratory rats may not differ. There is less individual variability within the measures IL, PEI and EF. It is possible that the differences seen between the two species with regard to these measures may be due to real species differences. It is also possible that the differences, should they prove to be reliable, are not due to species differences but to the effects of domestication on the behavior of laboratory rats. There are at present no data on the copulatory behavior of wild Rattus norvegicus and it is possible that wild Norway rats are even more similar to wild roof rats than are domesticated Norway rats. Comparisons among wild and domesticated stocks of Norway rats and wild stocks of roof rats would provide evidence for this suggestion.

It can be concluded from this comparison of the quantitative measures of copulatory behavior of roof rats and laboratory rats that in five of the eight measures compared there appears to be very little difference between the two

species. With regard to the other three measures, roof rats and laboratory rats do not appear radically different, but small reliable species differences might exist.

With regard to changes that occur in the copulatory behavior of roof rats as exhaustion is approached, a similar conclusion can be drawn. The curves generated for IF, EL, MIII and PEI in Figures 1-4 for roof rats are almost identical in form to those presented by Karen and Barfield (1975) for laboratory rats. They are also similar in form to those functions described by Dewsbury (1968) for laboratory rats using a slightly different method of presentation and to those presented by Larsson (1956). It should be noted that Larsson did not in fact conduct standard satiety tests with his animals but only tested the animals for a one hour period. Nevertheless Larsson's functions for the measures IF, EL and PEI are strikingly similar to the present ones for roof rats. These facts suggest that similar mechanisms underly the sexual arousal and exhaustion of roof rats and laboratory rats. Theoretical speculations concerning the nature of these mechanisms can be found in papers by Beach (1956), Beach and Jordan (1956), Beach and Whalen (1959), Dewsbury (1968), Karen and Barfield (1975), and McGill (1965).

Categorization of Behavior

A categorization of the behaviors accompanying copulation was made on one test each for 11 males and 11 females. A twelfth pair of animals was not categorized due to the death of the male prior to categorization.

Figures 5 and 6 present the categorization data for males and females, respectively. Data from 15 of the possible 16 mutually exclusive categories of male behavior are presented in Figure 5. The sixteenth category, Dig, was never found to occur more than 1% of the time and was dropped from further analysis. The data in Figure 5 are presented as per cent of time spent in each category during the IL, first, second and last EL, first and second PEI and the 30 minute satiety criterion. All of the periods are further divided into quarters with the exception of the IL. The data are expressed as means and standard errors.

During the intromission latency period males spent about 85% of their time in activities directed at the female: sniffing, genital and general grooming and chasing. Particularly frequent were the episodes of sniffing and chasing. The EL periods were predominated by copulation related activities such as chasing, mounting, pulling on the female, sniffing and genital grooming of the female. Males also spent extended periods of time grooming their own genitals; an activity highly associated with copulatory activity. Males spent from 13-23% of their time in locomotor exploratory behavior and 6-17% of their time sitting. The majority of the postejaculatory intervals were spent in activities such as locomotor-exploratory behavior, sitting and general grooming. Fourteen percent of the time was spent in genital grooming and only 2-4% of the time was spent chasing and mounting females. Grooming and sniffing females

Figure 5. Categorization of male copulatory behavior. Each measure is expressed as percent of total time for each quarter of each time period. Data are presented as means and standard errors.

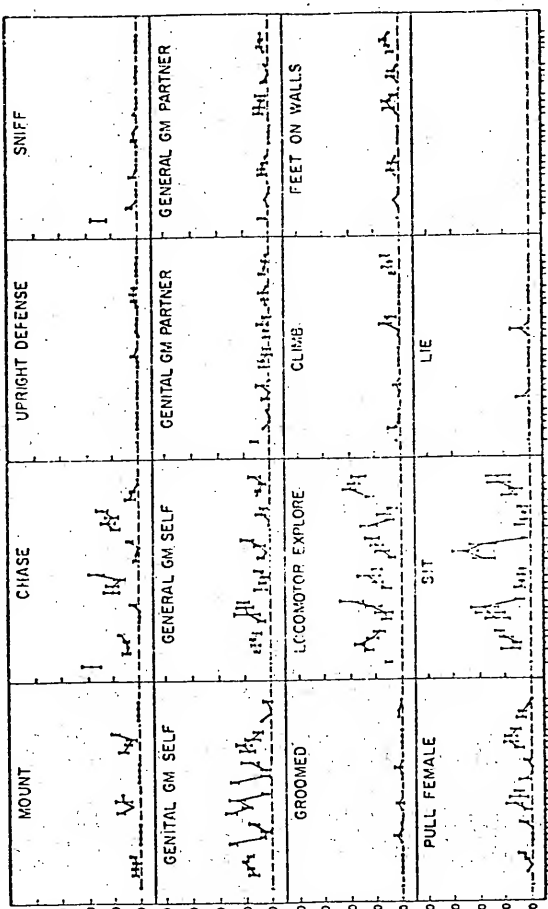
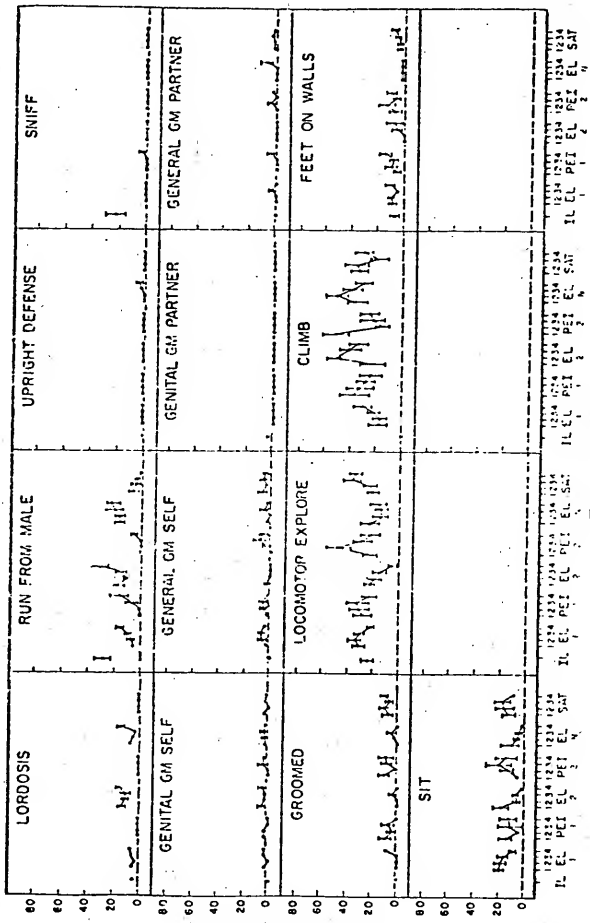

MOUNT
CHASE
UPRIGHT DEFENSE
SNIFF
GENITAL GM SELF
GENERAL GM SELF
GENITAL GM PARTNER
GENERAL GM PARTNER
GROOMED
LOCOMOTOR EXPLORE
CLIMB
FEET ON WALLS
PULL FEMALE
SIT
LIE
PERCENT OF TIME
IL EL PEI EL SAT
TIME PERIOD

Figure 6. Categorization of female copulatory behavior. Each measure is expressed as percent of total time for each quarter of each time period. Data are presented as means and standard errors.


LORDOSIS
RUN FROM MALE
UPRIGHT DEFENSE
SNIFF
GENITAL GM SELF
GENERAL GM SELF
GENITAL GM PARTNER
GENERAL GM PARTNER
GROOMED
LOCOMOTOR EXPLORE
CLIMB
FEET ON WALLS
SIT
PERCENT OF TIME
TIME PERIOD

occupied 7-13% of the time. Mounting and chasing both tended to occur in the final quarter of the PEI just prior to the next series. Very little time was devoted to copulation-related activities such as chasing and mounting during the satiety period as compared to the EL periods. What copulation-related acitivity did occur was restricted to the first two quarters only. About 65% of the period was taken up with locomotor-exploratory behaviors and sitting.

Figure 6 presents the percent of time females spent in 13 of the 15 possible categories of female behavior. The data are presented as means and standard errors. The categories of Dig and Lie were excluded because during no period did either category occupy more than 1% of the time. During the IL period females behavior appeared to be directed at the male. Sniffing, genital and general grooming, being groomed, upright defense, running from the male and lordosis accounted for 58% of the period. The remainder of the period was spent in locomotor-exploratory behaviors, feet on walls and climbing. Females spent from 16-35% of their time during the EL periods in active copulation or activities involving the male-including running, lordosis, being groomed, upright defense and grooming the male. Sitting and locomotor-exploratory activities (not including climbing) accounted for 25-53% of the females' time in this period. Climbing behavior was observed to occur interspersed in bouts of both locomotor-exploratory and copulatory behaviors. Often, especially in later series, females would climb on the cage top in an apparent attempt to avoid the chasing

male. Climbing was observed to occur from 22-38% of the time during EL periods. The majority of the two PEI periods were devoted to locomotor exploratory behaviors and climbing. Only 1-5% of the time was spent running from males or in lordosis; these behaviors occurred during the fourth quarter of the periods prior to the next series. During the satiety period females spent the majority of their time in locomotor-exploratory behaviors and climbing. Thirteen percent of the time was spent in sitting. Only 4% of the time was devoted to running from the male and lordosis; this occurred primarily during the first two quarters.

Figures 7 and 8 present the categorization data for males and females in a slightly different fashion but one that facilitates interspecific comparisons. For the males, 10 of the 15 categories presented in Figure 5 have been collapsed into six mutually exclusive categories and overall means calculated for each time period. The category locomotor-explore includes locomotor-explore, climb and feet on walls. Chase-mounts includes chase, mount and pull female. The categories general groom self, genital groom self, sniff and sit are the same as in Figure 5. For females 10 of the 13 categories in Figure 6 have been collapsed into nine categories in Figure 8. Locomotor-explore includes locomotor-explore and feet on walls. The categories run from male, lordosis, sniff, genital groom self, general groom self, climb and sit are the same as in Figure 6.

Figure 7. Collapsed data for categorization of male copulatory behavior. Each measure is expressed as percent of total time for each time period. Data are presented as means and standard errors.

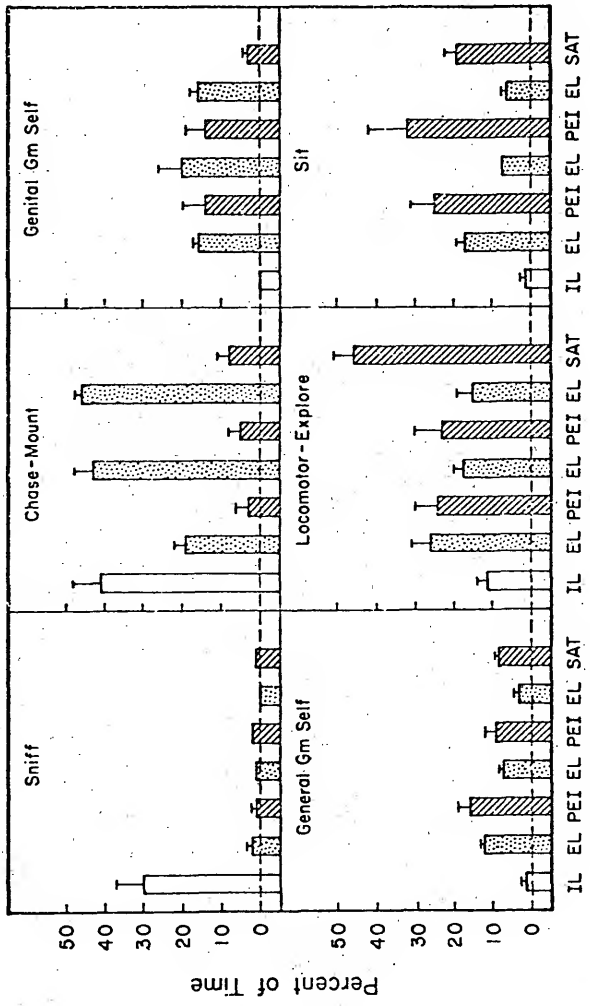
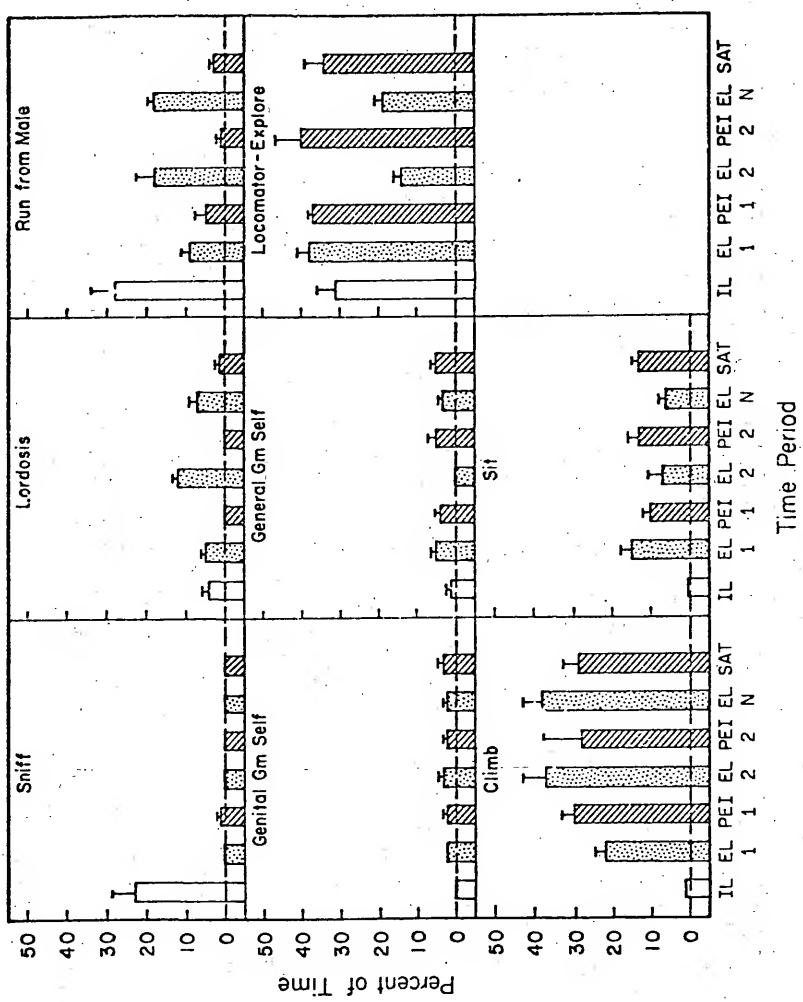

Sniff
Chase-Mount
Genital Gm Self
General Gm Self
Locomotor-Explore
Sit
Percent of Time
0
10
20
30
40
50
IL EL PEI EL EL SAT
1 1 2 2 N
Time Period

Figure 8. Collapsed data for categorization of female copulatory behavior. Each measure is expressed as percent of total time for each time period. Data are presented as means and standard errors.


Sniff
Lordosis
Run from Male
Genital Gm Self
General Gm Self
Locomotor-Explore
Climb
Sit
Percent of Time
0
10
20
30
40
50
IL EL PEI EL PEI EL SAT
1 1 2 2 N
Time Period

The collection of categorization data for laboratory rats by Dewsbury (1967) allows detailed comparisons to be made with the present data for roof rats. A few qualitative and quantitative differences in behavior between the two species are apparent. However, as with the other aspects of copulatory behavior discussed thus far, the most striking features of these comparisons are the great similarities in behavior. The copulation-related behaviors of chase-mount in males and lordosis in females were almost identical in quantitative as well as qualitative comparisons between the two species. Similarly the behaviors of sniffing, locomotor-explore and non-genital grooming, are quite similar for males of both species. The patterns of genital grooming and general grooming, sitting, upright defense and lying down were also similar for females of both species.

The patterns of change in behaviors across time periods (i.e., from IL to EL to PEI) within the first series were very similar for males of both species with regard to the behaviors genital grooming and sitting. Both species showed more genital grooming during the EL period and more sitting during the PEI period. Patterns of change across time periods were also very similar for laboratory rats and roof rat females for the behaviors sniffing, run from male and locomotor-explore.

Quantitatively, laboratory rat males tended to spend more time genital grooming during EL and PEI periods than did roof rat males. However, roof rat males tended to spend

more time sitting during these two periods than did laboratory rat males. Female roof rats tended to spend much more time running from males during the IL and EL periods than did female laboratory rats. However, female laboratory rats tended to spend about twice as much time in locomotor-exploratory activities during all time periods than did female roof rats.

Qualitatively, the only major differences between the two species appears to be with regard to the occurrence of allo-grooming in roof rats. Male and female laboratory rats are not reported to engage in genital and general grooming of the partner while male and female roof rats engage in low but consistent levels of these behaviors. Climbing behavior is also not reported for laboratory rats; however, Dewsbury's testing situation provided no opportunity for his subjects to climb. It is doubtful whether they would climb even if given the opportunity. On several occasions laboratory rats have been tested in the roof rat testing cages and at no time have laboratory rats been observed to climb on the cage top.

Quantitatively and qualitatively roof rats appear very similar to laboratory rats with regard to the behaviors accompanying copulation. The differences between laboratory rat and roof rat females in running from the male may be related to the occurrence of the darting, ear wiggling and tail rattling pattern observed in female roof rats that was discussed earlier. The occurrence of this presumed solicitation pattern may indicate a real species difference

between roof rats and Norway rats. It may be that roof rat males require more stimulation from the female in order to initiate copulation than do laboratory rats. It is also possible that the same behavior patterns occur in wild Norway rats but that through domestication, these patterns have been lost. There are no clear explanations for the other differences observed between the two species.

Ultrasonic Vocalizations

Ultrasonic vocalizations were observed on a total of 22 tests for 11 pairs of animals, each pair being observed on two tests. These were the same tests during which the categorizations of behavior were done: the fifth and sixth positive tests for each pair. Identification of individual animals producing ultrasonic vocalizations in social situations is sometimes difficult because such vocalizations can be produced by more than one animal at one time in a given test. Using only the ultrasonic receiver it is impossible to localize the sounds well enough to positively identify the source of the vocalizations. In most cases, however, it was possible to correlate the occurrence of the ultrasonic vocalization with rhythmic chest movements in one but not the other animal. These chest movements, probably rhythmic exhalations producing the vocalizations, are also seen in isolated animals during vocalizations. Singing was never observed to occur in the absence of such chest movements by one or the other animal.

During pretesting, scans of the frequency range from 20 kHz to 60 kHz during various phases of the copulatory sequence revealed the only observable vocalizations to occur at approximately 28 kHz. As a result during actual testing the frequency dial of the ultrasonic receiver was set at about 28 kHz and the occurrence and duration of all vocalizations occurring in this range were recorded on one channel of the event recorder. This procedure minimized the probabilities of detecting ultrasonic vocalizations occurring at other frequencies and it is therefore possible that vocalizations were made at other frequencies but went undetected. Sewell (1967) for example reports male vocalizations in the 50 kHz range during mounting activity in laboratory rats.

Both males and females were observed to emit ultrasonic vocalizations during copulatory sequences. For both males and females, vocalizations were observed at 28 ± 5 kHz in frequency. These vocalizations occurred in pulses of 1-3 sec in length with pulses occurring in trains of variable length; some up to 3 min in length on occasion.

Some sex differences were noted in the occurrence of ultrasonic vocalizations. Males were observed to vocalize only during PEIs and the satiety criterion period. Ultrasonic vocalizations followed 91% of the 83 total ejaculations observed on these 22 tests. On 8 tests male vocalizations were observed that were not directly associated with ejaculations or other copulatory activities.

All of these vocalizations occurred during the satiety criterion period. Twenty-two percent of these vocalizations appeared to be correlated with sudden noises occurring in the testing room.

Twenty-five instances of female vocalization were observed on 14 of the 22 tests. Female vocalizations, unlike male vocalizations, were observed during EL periods as well as PEI periods and the satiety periods. However, only 24% of the females' vocalizations occurred during EL periods; the other 75% occurred during PEIs and the satiety period. Only 20% of all female vocalizations appeared to be correlated with sudden noises.

Table 5 presents quantitative data (means and standard errors) on male postejaculatory vocalizations from eight subjects on 16 tests. Only those subjects having at least three series on both tests were included in order to facilitate analysis of changes in behavior across series. The measures of vocalization and other copulatory measures have been defined previously. The numbers in parentheses are means and standard errors for data collected by Barfield and Geyer (1975) on laboratory rats and have been included to facilitate cross-species comparisons.

As can be seen from the table, the measures IF and EL show significant decreases from first to second series. The measures VT and PEI show significant increases from first to second series. The measures VL, PEI-VT and VT/PEI do not change significantly from first to second series. It

Table 5

Means and Standard Errors of the Quantitative Measures of Male Postejaculatory Vocalization and Other Measures of Copulatory Behavior and Results of T-tests

Behavioral Measure	Series 1	Series 2	t-test for related pairs (df = 7)
IL	(174.6 ± 45.6) 45.0 ± 19.8	---------- ----------	--------
IF	(11.1 ± 1.5) 8.8 ± 1.0	(5.2 ± 0.5) 3.4 ± 0.3	t = 5.35 **
EL	(859.0 ± 121.0) 595.9 ± 152.5	(337.0 ± 33.8) 106.9 ± 12.5	t = 3.05 *
VL	(36.0 ± 4.0) 36.4 ± 6.8	(42.8 ± 10.2) 41.4 ± 5.7	t = 0.65
VT	(328.0 ± 14.9) 161.6 ± 18.9	(415.0 ± 19.0) 210.5 ± 25.5	t = 3.16 *
PEI	(429.0 ± 18.9) 256.8 ± 19.0	(528.0 ± 19.9) 294.9 ± 20.2	t = 4.58 **
PEI-VT	(101.0 ± 15.1) 95.2 ± 17.6	(117.0 ± 18.5) 85.0 ± 15.5	t = 0.89
VT-PEI	(0.77 ± 0.03) 0.63 ± 0.07	(0.79 ± 0.3) 0.71 ± 0.06	t = 1.84

Note: N = 8, 2 tests per animal.

Measures in parentheses are for Norway rats from Barfield and Geyer, 1975.

* $p < .02$
** $p < .01$

takes male roof rats from 36-41 sec to initiate ultrasonic vocalizations following an ejaculation and such vocalizations continue for 2.5 to 3 min. Roof rat males spend from 63-71% of their total PEI in vocalization activity.

When the present data are compared to those of Barfield and Geyer (1975) for laboratory rats, striking similarities are seen between the two species. The measures VL and PEI/VT are almost identical in the two species. Laboratory rats tend to spend more absolute time in vocalization than do roof rats, as measured by VT. However, the total PEIs for laboratory rats are considerably longer than those of roof rats. When the percent of the PEI spent in vocalization is examined it reveals a much closer similarity between the two species. Roof rats spend 63% of their first PEI in vocalization; laboratory rats spend 77%. Roof rats spend 71% of their second PEI in vocalization, laboratory rats 79%.

It has been suggested that in laboratory rats the measures VT and PEI/VT are fair estimates of the absolute and relative postejaculatory refractory periods, respectively (Barfield & Geyer, 1975; Karen & Barfield, 1975). Similarly VT/PEI has been suggested to be a reasonable estimate of the percentage of the PEI taken up by the absolute refractory period. Again, the close correspondence between these two species with regard to these measures suggests that similar mechanisms underlie the arousal, maintenance and exhaustion of their copulatory behavior.

Barfield and Geyer (1972, 1975) report that male laboratory rats are most often inactive during ultrasonic vocalizations, lying quietly or occasionally grooming themselves or moving slowly about. Similar behavior for female laboratory rats during male ultrasound is also reported by these authors with females reported "...also often quiescent"(Barfield & Geyer, 1975, p. 726). The collection of categorization data concurrently with ultrasonic vocalization data provides an excellent opportunity to quantify the behaviors of male and female roof rats during ultrasonic vocalizations.

The behavior of 11 males and 11 females during male postejaculatory vocalizations was categorized on one test for each male and each female. The per cent of time males spent in six categories of behavior during the first, second and terminal PEI vocalizations is presented in Figure 9. The per cent of time spent by females in eight categories of behavior during the male's first, second and terminal PEI vocalizations are presented in Figure 10. Only six of the possible 16 categories of male behavior and only eight of the possible 15 categories of female behavior are presented because in both cases the remaining behaviors occurred no more than 1% of the time.

Figure 9 reveals that male roof rats spent the majority of their vocalization time sitting. The percentage of vocalization time spent sitting increased over successive series. Less than 12% of the vocalization time was spent in

Figure 9. Categorization of male behavior during male postejaculatory songs. Each measure is expressed as percent of total time for each PEI period. Data are presented as means and standard errors.

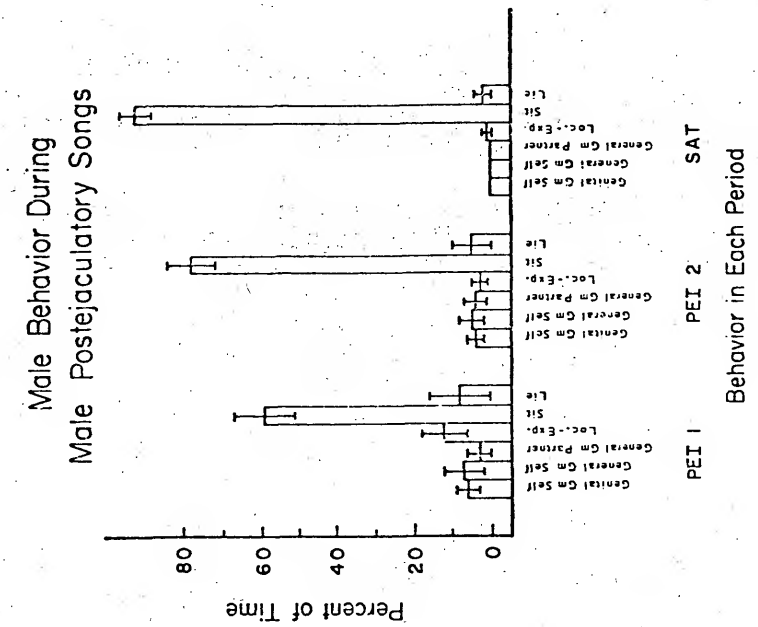
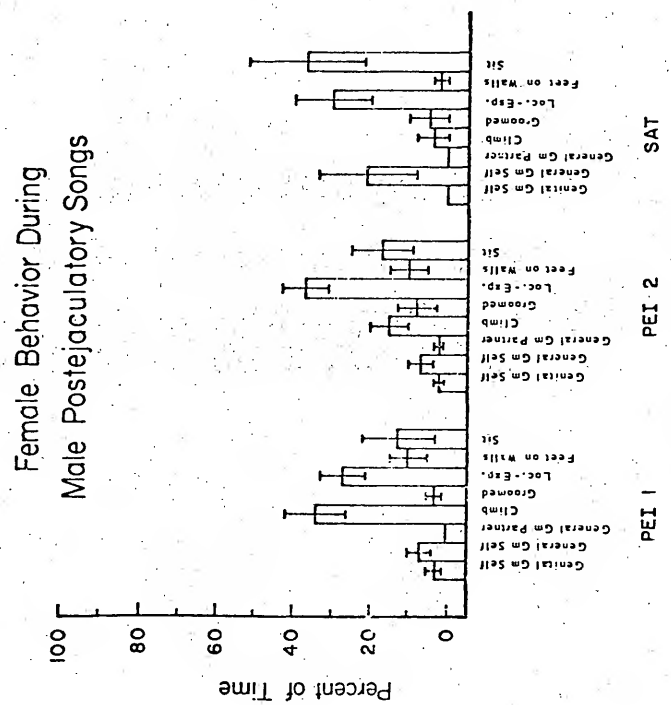

Male Behavior During
Male Postejaculatory Songs
Percent of Time
0
20
40
60
80
Genital Gm Self
General Gm Self
General Gm Partner
Loc.-Exp.
Sit
Lie
PEI 1
PEI 2
SAT
Behavior in Each Period

Figure 10. Categorization of female behavior during male postejaculatory songs. Each measure is expressed as percent of total time for each PEI period. Data are presented as means and standard errors.


Female Behavior During
Male Postejaculatory Songs
Percent of Time
100
80
60
40
20
0
Genital Gm Self
General Gm Self
General Gm Partner
Climb
Groomed
Loc.-Exp.
Feet on Walls
Sit
PEI 1
PEI 2
SAT
Behavior in Each Period

locomotor-exploratory behavior, the remainder was spent in quiescent activities such as grooming, sitting and lying. This is very similar to the reports of Barfield and Geyer (1972, 1975) with regard to laboratory rat activities during vocalization. One point of difference is worthy of note. Barfield and Geyer report that laboratory rats spend much of their vocalization time lying down. Roof rats spend very little of their vocalization time lying down. During the majority of their vocalization time, male roof rats sit in a relaxed but alert posture. Indeed, on several occasions vocalizations were observed to be interrupted for short periods of time by sudden noises in the testing room. Male roof rats appeared to be immobile during periods of vocalization, but are not totally unresponsive to environmental stimuli.

The activities of female roof rats during male vocalizations appear to be more variable. Figure 10 shows that female roof rats spent the majority of the vocalization time in such non-quiescent activities as locomotor-exploratory behavior, feet on walls and climbing during the first two vocalizations. However, during the last vocalization, females spent much more of their time in such quiescent activities as sitting and self-grooming. Female roof rats appear to be much more active than female laboratory rats during the early postejaculatory vocalizations of the male. However, during the final postejaculatory vocalizations, female roof rats appear more similar to female laboratory rats spending long periods of time in quiescent behaviors.

Overall, the postejaculatory vocalizations of roof rats appear remarkably similar to those reported for laboratory rats in their quality and their temporal patterning.

The biological function of male postejaculatory vocalizations is not clear. Barfield and Geyer (1972) note that in laboratory rats 22 kHz vocalizations can be observed in a number of different social situations. They suggest that the 22 kHz frequency may be "a ...'carrier frequency' for signals denoting states of contact avoidance" (p. 1350). Specifically in sexual situations they suggest it may function to inhibit female sexual behavior during periods when the male is incapable of sexual activity. In a later paper (Barfield & Geyer, 1975) they suggested that the postejaculatory vocalizations might have a facilitative effect on reproduction by affecting the reproductive physiology of the female. Barfield and Geyer also noted that sounds have been shown to be significant in initiating specific reproductive responses in the females of some species of birds (Barfield, 1971). It was suggested that postejaculatory vocalizations by male rats may have a similar function. Another possibility not mentioned by Barfield and Geyer concerns the reduction of competition between conspecific males. If 22 kHz vocalizations really do communicate a state of contact avoidance in laboratory rats it is quite possible that this might keep other conspecific males away from the vocalizing male and the female with which he is mating. This might prevent a take-over of the female by a strange

male when the vocalizing male is incapable of sexual activity, thereby reducing competition between the vocalizing male and others. Further research should clarify the adaptive significance of posejaculatory vocalizations in the reproductive process.

EXPERIMENT 2

The results of Experiment 1 demonstrated that the copulatory behavior of roof rats is fundamentally the same as that of laboratory rats. However, the first experiment did not provide any indication as to the importance of various aspects of the male's behavior in the initiation of successful pregnancy in female roof rats. As was pointed out earlier, Adler (1969), Chester and Zucker (1970) and others have shown that for laboratory rats, a single ejaculatory series provides sufficient stimulation to induce successful pregnancy in 80-90% of the females. In contrast, Dewsbury and Estep (1975) and Lanier et al. (in press) have demonstrated that in cactus mice (Peromyscus eremicus) and Syrian golden hamsters (Mesocricetus auratus), copulations beyond the first ejaculation are essential to maximize the probability of successful pregnancy. Although roof rats appear quite similar to laboratory rats in their copulatory behavior, it is possible that quite different aspects of the copulatory pattern are important for successful pregnancy in roof rats. The present experiment was designed to assess the significance of multiple ejaculations in the initiation of pregnancy in roof rats. Comparisons are made between females given just one ejaculation and those given a complete satiety test with regard to the initiation of pregnancy.

Materials and Methods

Subjects

The subjects of Experiment 2 were nine male and sixteen female laboratory-reared offspring of wild trapped roof rats. All of these animals were bred, weaned, and maintained in the same fashion as those of Experiment 1.

Apparatus

Behavioral tests were conducted in the same clear, plastic cages as used in Experiment 1. Behavioral events were also recorded in the same fashion as Experiment 1 using the event recorder.

Procedures

Daily vaginal smears were taken on all females starting when the females were 60 days of age and continuing throughout the study. Smears were taken between 0800 and 1100 hrs using a thin wire loop. These vaginal smears were examined microscopically and a determination was made of the stage of the female's estrous cycle on the basis of the cell types present in the smear. The stages of the estrous cycle were classified according to the criteria used by Hardy (1972) for laboratory rats. These were: proestrus, predominance of nucleated epithelial cells; estrus, predominance of cornified epithelial cells; metestrus, cornified and nucleated epithelial cells and some leucocytes; diestrus, preponderance of leucocytes with some nucleated epithelial cells.

After the females began to show regularity in their estrous cycles, they were pretested for copulatory behavior and fertility. On the afternoon of vaginal proestrus, the proestrus female was placed in a testing cage with a male and, if receptive, was allowed to mate for at least three copulatory series. If the female was not behaviorally receptive, she was returned to her home cage and retested at the next occurrence of vaginal proestrus. Those females showing no regular estrous cycles, having three consecutive negative tests, or mating but not becoming pregnant and delivering pups after two mating tests were eliminated from the study. This system of pretesting allowed positive verification of fertility for both males and females and allowed both males and females to gain experience in the standard testing situation.

Females judged fertile by this method and which demonstrated two consecutive estrous cycles of 3-5 days duration were tested twice, once in each of two conditions. Half of the females were randomly assigned to first serve in the one ejaculation condition (1 Ejac), the other half served first in the satiety condition (Satiety). The design was counterbalanced so that those animals tested in the 1 Ejac condition on their first test served in the Satiety condition on their second test and vice versa. All of the animals were between 123 and 192 days of age at the time of their first test and between 179 and 240 days of age at the time of their second test.

Mating tests were conducted on the afternoon of vaginal proestrus approximately three hours into the dark phase of the light cycle. The testing procedure was similar to that of Experiment 1 with males introduced into the test cages 5-10 minutes before the females. Testing started with the introduction of the female. If the male failed to gain an intromission within 30 minutes after the start of the test, the test was terminated and the female was retested at the next occurrence of vaginal proestrus.

Each female assigned to the 1 Ejac condition was allowed to mate with a proven fertile male until he had achieved one ejaculation. At this point the test was terminated and the female was returned to her home cage. Each female assigned to the Satiety condition was allowed to mate with a proven fertile male until he had reached an arbitrary satiety criterion of 30 minutes without an intromission. The test was terminated at this time and the female was returned to her home cage.

Following a positive test a female continued to receive daily vaginal smears and the presence or absence of regular estrous cycles was noted. Females not becoming pregnant were allowed to display at least 2 complete 3-5 days cycles before being retested. Those becoming pregnant were allowed to deliver their litter, then retested after the resumption of regular 3-5 day estrous cycle activity. Females displaying at least 12 consecutive days of diestrus following a positive mating test but not delivering pups were judged to be

pseudopregnant. Those displaying diestrous smears for 20 consecutive days and delivering pups between days 21 and 22 were judged to have become pregnant as a result of the mating. Those females continuing to show regular 3-5 day cycles following mating were judged to be neither pregnant nor pseudopregnant.

Behavioral Measures

The standard measures of copulatory behavior were taken on all tests.

Results and Discussion

A total of 16 females completed both tests and are included in the final data analysis. Table 6 presents the percentages of tests in which females became pregnant, pseudopregnant or continued to cycle as a result of receiving one ejaculation or satiety. A binomial test (Siegel, 1956) for the proportions of females becoming pregnant in each of the two test conditions, revealed that there was no significant difference between the 1 Ejac and Satiety conditions in the proportions of females becoming pregnant ($X = 1$, $N = 7$; $p = .06$, 1-tailed). A binomial test for the proportions of females becoming pregnant in each testing order also revealed no significant differences ($X = 2$, $N = 7$; $p = .45$, 2-tailed).

Although there were no statistically significant differences between the 1 Ejac condition and the Satiety condition in the proportion of females becoming pregnant,

Table 6

Percent of Tests in Which Females Became Pregnant, Pseudopregnant or Continued to Cycle as a Result of Differing Amounts of Copulatory Stimulation

Outcome	1 Ejaculation[a]	Satiety[b]
% Pregnant	56	87
% Pseudopregnant	13	13
% Cycling	31	0
Mean Litter Size	8.0 ± 0.6 ($\underline{n}$ = 9)	7.1 ± 0.7 ($\underline{n}$ = 14)

Note. $\underline{n}$ = 16 for each condition except as noted for litter size data

[a] IF = 9.5

[b] EF = 5.4

it is interesting to note that there appeared to be a trend for a higher proportion of females to become pregnant after receiving multiple ejaculations. Also worthy of note is the fact that all of the females allowed to mate to satiety showed a progestational response (pseudopregnancy or pregnancy) while only 68% of those females receiving one ejaculatory series showed a progestational response. This response is an essential prerequisite for normal pregnancy in the female laboratory rat and, it can be assumed, for all female mammals not having a functional luteal phase in their estrous cycles, such as roof rats.

A *t*-test for unrelated samples comparing litter sizes for those females that had litters in each condition, revealed no significant differences in litter size as a function of different numbers of ejaculations $t(21 = 0.96$; $p < .05$, 1-tailed).

Table 7 reveals that within the 1 Ejac condition there was a trend for females receiving high numbers of intromissions to become pregnant or pseudopregnant while those receiving few intromissions prior to ejaculation tended to continue cycling. A *t*-test for unrelated samples indicated that those females becoming progestational had significantly more preejaculatory intromissions than those females continuing to cycle (Mean IF for progestational females 11.7, Mean IF for cycling females 5.4, $t(14) = 5.06$, $p < .001$).

Thus, as in laboratory rats, there appears to be a direct relationship between the amount of copulatory

Table 7

Mean IF and Resultant Female Response in 1 Ejaculation Condition

Outcome	n	IF[a]
Pregnant	9	11.4 ± 0.8
Pseudopregnant	2	13.0 ± 1.0
Cycling	5	5.4 ± 1.0

[a] Data presented as means and standard errors

stimulation received by a female and the probability that she will become pregnant. Although roof rat females can become pregnant after a single ejaculation provided that they receive a sufficiently high number of preejaculatory intromissions, in the average first series females only receive 7.4 - 10.1 intromissions. In the present experiment the average first ejaculatory series provided only enough stimulation to induce pregnancy in 56% of the roof rats so stimulated. This percentage was increased to 87% when the copulatory stimulation was increased to satiety, an average of 5.4 ejaculations. Because there was no statistically significant difference between the Satiety and 1 Ejac conditions with regard to the proportion of females that became pregnant, it appears that like Norway rats, roof rats reach maximal probabilities of pregnancy with a single ejaculatory series. However, it is difficult to believe that the 56% pregnancy rate in the 1 Ejac condition constitutes the maximal probabilities of pregnancy. It is quite possible that given a larger sample size the proportion of females pregnant in the 1 Ejac condition would be significantly different from the proportion of females pregnant in the Satiety condition.

It should also be noted that all of the work done thus far by Adler, Chester and Zucker and others on the functions of multiple ejaculations in Rattus norvegicus has been done on domesticated forms. To date no one has examined the functions of multiple ejaculations in wild Rattus norvegicus.

It is possible that the lack of a function for multiple series in this species, with regard to the induction of pregnancy, is an effect of domestication. That is, multiple ejaculations may be necessary for the induction of pregnancy in wild Norway rats but through the process of domestication this function has been lost. Domestication has been found to affect a wide variety of behaviors in both Norway rats and house mice (Mus musculus)(Barnett, 1963; Boice, 1972,1973; Lockard, 1968; Smith, 1972). There is even some evidence to suggest that domestication has affected the copulatory behavior of house mice (Estep, Lanier & Dewsbury, in press). Research on the induction of pregnancy in wild Norway rats should provide evidence to confirm or deny the possibility that domestication has affected the stimulus requirements for the normal initiation of pregnancy in this species.

The 32 tests of copulatory behavior conducted in this experiment provide an opportunity to compare the behavior of male roof rats paired with females in natural estrus to those paired with females in an artificially induced estrus. The females tested in this experiment were of necessity in natural estrus while those in Experiment 1 were brought into estrus with the aid of exogenous hormones.

Tables 8 and 9 present data from males mated with hormone-induced estrous females from Experiment 1 and data from males mated with females in natural estrus from the 1 Ejac and Satiety conditions, of the present experiment. In Table 8 means and standard errors for the latency measures

Table 8

Comparison of the Behavior of Males Tested with Females in Artificial vs Natural Estrus for Measures in the First Series

Behavioral Measure	Artificial Estrus	Natural Estrus	
		Satiety	1 Ejac
ML[a]	98.5 ± 18.6	104.8 ± 21.1	85.6 ± 19.9
IL[a]	146.3 ± 28.0	124.6 ± 30.2	96.9 ± 20.6
EF	4.3 ± 0.4	5.4 ± 0.4	----------
MF	5.1 ± 1.2	3.7 ± 0.7	8.1 ± 3.1
IF	7.6 ± 0.7	10.1 ± 0.8	9.5 ± 0.9
EL[a]	563.4 ± 118.5	621.8 ± 86.1	863.7 ± 176.1
MIII[a]	70.3 ± 9.3	64.0 ± 7.6	82.7 ± 12.6
PEI[a]	269.2 ± 15.5	281.1 ± 18.9	----------

Note. All data presented as means and standard errors

[a] All time measures expressed in seconds

Table 9

Comparisons of the Behavior of Males Tested with Females in Artificial vs Natural Estrus for Measures in Later Series

Measure	Series									
	2		3		N-2		N-1		N	
	A	N	A	N	A	N	A	N	A	N
MF	4.3 ± 2.0	1.9 ± 0.6	3.6 ± 0.9	2.2 ± 0.7	3.5 ± 0.9	2.4 ± 0.7	3.6 ± 1.0	3.3 ± 1.3	5.7 ± 2.3	5.6 ± 1.7
IF	2.8 ± 0.3	2.4 ± 0.2	3.0 ± 0.2	2.7 ± 0.3	4.4 ± 0.2	3.1 ± 0.3	3.8 ± 0.3	3.2 ± 0.3	3.3 ± 0.3	4.7 ± 0.7
EL[a]	170.8 ±39.1	82.1 ±14.8	166.5 ±28.1	91.7 ±12.4	226.1 ±39.1	102.4 ±13.7	262.2 ±86.5	139.8 ±17.6	340.4 ±62.3	411.2 ±64.6
MIII[a]	66.3 ±14.5	33.4 ± 5.2	69.6 ±13.3	35.3 ± 3.9	50.0 ± 7.6	34.6 ± 4.5	52.5 ± 7.6	47.1 ± 5.9	112.4 ±22.4	92.8 ±14.6
PEI[a]	308.5 ±19.4	298.4 ±14.8	358.6 ±27.5	345.6 ±16.0	370.8 ±17.0	453.2 ±18.4	497.2 ±32.0	497.2 ±44.5	----- -----	----- -----

Note. A = Artificial Estrus, N = Natural Estrus

All data presented as means and standard errors

[a] All time measures expressed in seconds

and the measures of the first ejaculatory series are presented. The data on artificial estrous behavior came from Table 1 of the first experiment and are based on 71 tests from twelve pairs of animals. The data on natural estrous behavior came from the present experiment and are based on sixteen pairs of animals, each tested once in both conditions.

Analyses of variance were performed to determine whether estrous state of the female did in fact affect the standard measures of copulatory behavior. The data for artificial estrous tests were from Experiment 1. Data from the first two series of the first test from all twelve pairs of animals were used. In Experiment 2, t-tests for related samples indicated that there were no significant differences between the 1 Ejac condition and the Satiety condition for the eight standard measures of copulatory behavior. As a result, the data from the first two series on the 16 tests of the Satiety condition constituted the data for the natural estrous condition. One-way analyses of variance were applied to the measures occurring only once per test (i.e., ML, IL and EF). Two way analyses of variance were used on the remaining measures that occurred more than once per test. The results of these analyses of variance can be seen in Table 10. Complete ANOVA tables appear in Appendix B. As can be seen from Table 10, significant changes from first to second series can been seen for the measures MF, IF and MIII. Estrous condition of the female apparently

Table 10

Results of Analyses of Variance
Comparing Different Estrus Conditions

Behavioral Measure	df	F	p[a]
ML	1,26	2.15	NS
IL	1,26	4.52	$<.05$
EF	1,26	2.42	NS
MF			
Estrus Condition	1,26	0.38	NS
Series	1,27	15.07	$<.001$
Series x Condition	1,27	1.45	NS
IF			
Estrus Condition	1,26	7.96	$<.01$
Series	1,27	101.58	$<.001$
Series x Condition	1,27	9.07	$<.01$
EL			
Estrus Condition	1,26	0.19	NS
Series	1,27	0.26	NS
Series x Condition	1,27	0.003	NS
MIII			
Estrus Condition	1,26	3.25	NS
Series	1,27	5.15	$<.05$
Series x Condition	1,27	2.04	NS
PEI			
Estrus Condition	1,26	0.07	NS
Series	1,27	1.85	NS
Series x Condition	1,27	0.09	NS

[a] NS = Not significant

affected only two of the eight measures: IL and IF. For IL, males mated to natural estrous females initiated copulation much sooner than those males mated to females in artificial estrus (Mean IL, natural estrus = 124.5, Mean IL artificial estrus = 322.6). For the measure IF a significant interaction of estrous condition with series was found. Analyses of variance for simple effects of changes across series indicated that in both conditions there was a significant decrease in IF from first to second series (natural estrus $F(1,27) = 91.98$, $p < .001$; artificial estrus $F(1,27) = 18.67$, $p < .001$). However as multiple t-tests revealed, there was no significant difference in the second series IF between conditions ($t(27) = 0.1$), while the first series IF for the natural estrous condition was significantly larger than the first series IF for the artificial estrous condition ($t(27) = 3.8$, $p < .001$). This indicates that the interaction was due to a much greater drop in IF from first to second series in the natural estrous condition than in the artificial estrous condition. As there was no difference between estrous conditions with regard to the second series IF, estrous condition appears only to affect the first series IF.

It is not clear why estrous condition of the female should affect only the measures IL and the first series IF. If estrous condition had a general facilitory or inhibitory effect on the copulatory behavior of a given pair of animals it might be expected that several measures of

copulatory behavior would be affected, and that those measures would be affected in a similar fashion. This does not appear to be the case. While males who copulated with natural estrous females initiated copulation sooner than those mated with artificial estrous females, the males mated with natural estrous females required more intromissions in the first series to achieve ejaculation.

It is of interest to note that the first series IF of the animals in natural estrus in this experiment was much closer to the IF reported for laboratory rats than the first series IF for animals tested in artificial estrus. Adler (1969) and Wilson, Adler and Le Boeuf (1965) reported first series IFs for laboratory rats mated with females in natural estrus to be 10.3 and 9.4, respectively. In these two experiments such average IFs provided enough stimulation to induce pregnancy in 83-90% of the females. However, in roof rats one ejaculatory series with an average of 9.5 intromissions only induces pregnancy in 56% of the females. This discrepancy is most easily explained in terms of differential sensitivity on the part of the females of the two species. While an average of 10 intromissions maximizes the probabilities of pregnancy in laboratory rat females, an average of 10 intromissions does not appear to provide enough stimulation to maximize the probabilities of pregnancy in roof rat females. This observed difference between species in female sensitivity to comparable copulatory stimulation may be accounted for by one of two

possible reasons. First, the difference may reflect true species differences in female sensitivity. Alternatively, the difference may be due to an increased sensitivity on the part of laboratory rat females to male copulatory stimulation as a result of domestication.

The data in Table 8 are also of interest with regard to species differences between roof rats and laboratory rats in the quantitative measures of copulation. Comparisons of the quantitative data of Table 8 for natural estrous tests for roof rats with the data in Table 4 for laboratory rats reinforces the conclusions drawn earlier about possible species differences. It had been noted earlier that there was overlap between species in the means for ML and MIII when comparing laboratory rats in artificial estrus with roof rats in artificial estrus. This overlap becomes even more pronounced when the data for natural estrous copulations in roof rats are compared to the data for laboratory rats. Where no overlap was noted between species with regard to the measures MF, IF and EL in Table 4, the natural estrous data for roof rats presented in Table 8 shows an overlap with the laboratory rat data for these three measures. No overlap had been found previously with regard to the measures IL, PEI and EF and it was hypothesized that perhaps there might be real species differences with regard to these measures. When the data for natural estrous roof rats are compared to those for laboratory rats in artificial estrus there appears to be no evidence for

overlap with regard to the measures IL and PEI. The EF for natural estrous roof rats is higher than that for those tested in artificial estrus but it is still somewhat lower than that reported for sexually experienced laboratory rats. It should be obvious to the reader that the appropriate species comparisons are not of roof rats in natural estrus versus laboratory rats in artificial estrus, but rather both species in natural estrus. There are, however, no comparable data for laboratory rats in natural estrus, hence these interspecific comparisons must be interpreted with caution. It is possible that laboratory rats tested in natural estrus would show changes in their behavior that would make laboratory rats and roof rats appear less similar with regard to the quantitative measures of copulation. However, the intromission frequency data from Adler (1969) and Wilson et al. (1965) suggest that this may not be the case.

GENERAL DISCUSSION

The data presented in Experiments 1 and 2 provide a reasonably complete description of the various aspects of the copulatory behavior of wild roof rats. Before discussing the implications of these results it is perhaps wise to review briefly the findings of these two experiments.

The copulatory behavior of wild roof rats could be classified as pattern #13 or pattern #15 in Dewsbury's taxonomy of copulatory behavior. Roof rats have no copulatory lock and no intravaginal thrusting and they usually, but not always, have multiple intromissions prior to ejaculation. They typically have multiple ejaculations prior to sexual satiety. This is the same pattern seen in a number of muroid rodents including Norway rats. The basic motor patterns and postures of copulation are identical to those seen in Norway rats.

Quantitatively the patterns of copulation of Norway and roof rats also appear quite similar. Roof rats and Norway rats are probably not different with regard to five of the eight quantitative measures taken. There are possibly real species differences with regard to the measures IL, EF and PEI. Roof rats and laboratory rats show similar functional changes in the quantitative measures of copulation as they approach sexual satiety. This implies that the underlying

mechanisms controlling copulatory behavior are the same or at least very similar in the two species.

With regard to the behaviors accompanying copulation roof rats and laboratory rats again appear very similar. Roof rats engage in allogrooming and climbing behaviors not reported for Norway rats and female roof rats spend much more time running from males than do Norway rats. Female roof rats also display a pattern of darting and tail-rattling not seen in laboratory rats. The occurrence of the allogrooming and increased running on the part of females may indicate that more mutual stimulation is required to initiate copulation in this species than in Norway rats.

Wild roof rats emit ultrasonic vocalizations in sexual contexts with the majority of vocalizations occurring in males following ejaculations. This is similar to patterns of ultrasonic vocalization reported for laboratory rats. Roof rats vocalizations occur at 28 kHz, while Norway rat vocalizations tend to occur at 22 kHz. The quantitative measures of ultrasonic vocalizations are also quite similar between the two species. Like male Norway rats, male roof rats tend to be quiescent during vocalizations while female roof rats tend to be active during most male vocalizations.

With regard to the stimulation necessary for the initiation of pregnancy, roof rats and Norway rats again appear similar. In domesticated Norway rats one normal ejaculatory series provides sufficient stimulation to maximize the probabilities of pregnancy (Adler, 1969).

Results of statistical analyses indicate that in roof rats, one ejaculatory series may also maximize the probabilities of pregnancy. However, it appears that roof rat females may need more preejaculatory intromissions than Norway rat females in order to become pregnant and/or progestational. Further research is needed to clarify the exact nature of the relationship between copulatory stimulation and the initiation of pregnancy in wild roof rats.

Finally, it was observed that there may be a few differences between the copulatory behavior of male roof rats mated with natural estrous females and male roof rats mated with females in artificial estrus. The implications of these results were not clear.

Many of the results found in these two experiments were discussed in terms of comparisons with laboratory (Norway) rats. This was done for two reasons: first, many of the measures of copulatory behavior and most of the initial descriptions of copulatory behavior in muroid rodents were first done on Norway rats, making Norway rats the "standard" by which most other descriptions are compared. Second, there is an intrinsic interest in how the behavior of these two sympatric, closely related species compare. However, it is also of some interest to compare the behaviors of wild roof rats to the behaviors of other muroid rodents. Such comparisons can be made along a number of parameters such as the basic pattern of copulatory behavior, quantitative aspects of the pattern, et cetera. In this

discussion three such parameters will be considered: the basic pattern of copulation, the quantitative aspects of the copulatory pattern and the induction of pregnancy.

As had been noted earlier roof rats display pattern #13 copulatory behavior according to the taxonomy of copulatory behavior of Dewsbury (1972b). The data presented in that paper show that pattern #13 copulatory behavior is quite common among many species of muroid rodents for which the copulatory pattern is known. Thus roof rats do not appear to be radically different from many muroid species with regard to the basic pattern of copulatory behavior.

Comparisons of the quantitative aspects of the copulatory pattern make sense only when species are compared that have similar copulatory patterns (that is, when pattern #13 animals are compared to other pattern #13 animals). Table 11 presents quantitative data for the standard measures of copulatory behavior for nine muroid species that all display pattern #13 copulatory behavior. It should be clear from the data presented in this table that wild roof rats fall well within the range of scores of other muroid rodents on all of the standard measures of copulatory behavior. As with the qualitative aspects of copulatory behavior, roof rats do not appear to be very different from other muroid species with regard to the quantitative aspects of copulatory behavior.

Finally, we can compare roof rats with other muroid rodents with regard to the stimulation necessary for the initiation of pregnancy . Such data have been reported

Table 11

Comparisons of Standard Measures of Copulatory Behavior for the First Series Among Some Pattern #13 Muroid Rodents

	Behavioral Measure							
	ML[a]	IL[a]	EF	MF	IF	EL[a]	MIII[a]	PEI[a]
Rattus norvegicus[b]	-----	------	7.4	6.7	10.8	687.0	62.6	372.0
Rattus rattus	98.5	146.3	4.3	5.1	7.6	563.4	70.3	269.2
Meriones unguiculatus[c]	316.0	479.0	6.7	8.7	14.2	442.0	31.3	189.0
Mesocricetus auratus[d]	-----	117.0	9.8	---	14.2	199.5	12.1	47.9
Sigmodon hispidus[e]	235.3	263.4	2.1	0.3	4.5	230.3	54.7	484.7
Oryzomys palustris[f]	156.0	267.0	2.3	2.0	7.9	542.1	71.5	672.5
Peromyscus polionotus[g]	-----	2480.8	5.4	---	10.1	603.0	73.9	459.4
Peromyscus leucopus[h]	-----	1301.0	2.7	1.2	3.2	207.7	86.4	448.6
Peromyscus crinitus[i]	-----	1314.0	2.2	---	5.7	348.0	85.5	847.0

Note. All data presented as means.

a Time Measures in Seconds

b From Dewsbury, 1968

c From Davis et al., 1974

d From Unpublished Data

e From Dewsbury, 1972a

f From Dewsbury, 1970

g From Dewsbury, 1971

h From Dewsbury, in Press

i From Dewsbury, 1975a

thus far for only seven muroid species other than roof rats: Norway rats (Adler, 1969), Cactus mice (Dewsbury & Estep, 1975), Syrian golden hamsters (Lanier et al., in press), Montane voles (Davis, Gray, Zerylnick & Dewsbury, 1974), prairie voles (Gray, Zerylnick, Davis & Dewsbury, 1974), meadow voles (Gray, 1974) and house mice (McGill, 1970). In six of these eight species, extensive copulations occur after the first ejaculation. Only house mice and prairie voles tend to reach sexual satiety after completing just one or two ejaculatory series. In five of the six species that have extensive copulations beyond the first ejaculation, it appears that these extra copulations are essential to maximize the probabilities of pregnancy. In cactus mice, Syrian golden hamsters, montane voles and meadow voles, copulations beyond the first ejaculation appear to be necessary to maximize the probabilities of pregnancy in young virgin females (Davis et al., 1974; Dewsbury & Estep, 1975; Gray, 1974; Lanier et al., in press). In Norway rats, multiple ejaculations appear necessary to maximize the probabilities of pregnancy in old multiparious females but not young virgin females (Davis, 1974). It is possible that multiple ejaculations maximize the probabilities of pregnancy in roof rats as well. In prairie voles and house mice, species that do not usually have more than one or two ejaculatory series, maximal probabilities of pregnancy appear to be reached with a single ejaculatory series. This suggests that there is a fine co-adaptation within muroid species between male behavior and female reproductive physiology. In those species where stimulation beyond the first ejaculation is necessary to

maximize the probabilities of pregnancy, males usually provide that extra stimulation. In those species that do not need the extra stimulation to maximize the probabilities of pregnancy such stimulation is usually not given.

The differences in the copulatory behavior of roof rats and Norway rats alluded to throughout this paper do not appear to correspond in any meaningful way with the known differences in morphology, life history or ecology of these two species. Perhaps the most striking thing about the copulatory behavior of roof rats is the great similarity between roof rats and Norway rats. They are after all distinct species adapted to different ways of life and slightly different adaptive zones. Other closely related species are known to show more dramatic differences in their copulatory behavior than those observed here. Cactus mice (Peromyscus eremicus), California mice (Peromyscus californicus) and old field mice (Peromyscus polionotus) are all classified in the same genus, yet each shows a different pattern of copulatory behavior. Old field mice show pattern #13 characterized by no intravaginal thrusting, multiple intromissions and multiple ejaculations (Dewsbury, 1971). California mice on the other hand, show pattern #11 characterized by intravaginal thrusting, no multiple intromissions but multiple ejaculations (Dewsbury, 1974a). Cactus mice show yet another pattern of copulation, pattern #9, characterized by intravaginal thrusting, multiple intromissions and multiple ejaculations (Dewsbury, 1974b).

In light of such data the similarities between roof rats and Norway rats are most striking.

It should also be repeated that the differences and similarities seen between roof rats and Norway rats may not represent true species differences and similarities at all but rather reflect changes that have occurred in Norway rats as a result of domestication. There are at present no comparable quantitative data on the copulatory behavior of wild populations of Norway rats. Until these data are collected the differences and similarities between Norway rats and other species must be interpreted with caution.

It was noted in the Introduction that one of the reasons for the present study of the copulatory behavior of wild roof rats was to assess the possibility that a behavioral isolating mechanism might be responsible for the lack of hybridization between sympatric populations of roof rats and Norway rats. The present data show the copulatory behavior of roof rats and Norway rats to be very similar and provide no support for the notion that differences in copulatory behavior might act as behavioral isolating mechanisms between these two species. This does not deny the possibility that other behavioral isolating mechanisms might exist that keep the species from hybridizing. One such mechanism might be pheromonal in nature such that the members of one species would not be sexually attracted to members of the opposite sex of the other species.

It is also possible that copulation itself provides no isolating mechanism at all between the two species. Hybridization might be prevented by infertility or inviability of offspring produced by heterospecific matings. There is in fact some evidence to suggest that heterospecific matings between the two species produce no viable young. Gray (1972) cites several studies of attempted hybridization between roof rats and Norway rats. The better of these is a study by Hiraiwa and Yoshida (1956). Using artificial insemination techniques these authors report normal pregnancy-type weight gains in 26 of 48 Rattus rattus females inseminated with R. norvegicus sperm. However, half way through pregnancy all of these females showed bloody vaginal discharges and weight loss. No viable young were delivered of these inseminations. The eggs of six other inseminated females were examined soon after fertilization and found to be developing normally up to the second cleavage of the eggs. Hiraiwa and Yoshida interpreted these results as indicating that the females had become pregnant as a result of the heterospecific inseminations but that the embryos had died around the midpoint of gestation and had been reabsorbed.

Further study of the behavior of heterospecific pairs of Norway and roof rats might provide some indication of other possible isolating mechanisms. Pairings of estrous female Norway or roof rats with heterospecific males might provide some evidence for possible pheromonal, visual or auditory precopulatory isolating mechanisms. Such studies

could also provide further evidence for or against post-copulatory isolating mechanisms such as hybrid inviability.

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APPENDIX A

ANALYSES OF VARIANCE FOR EXPERIMENT 1

Table A-1

Analysis of Variance for ML

Source	df	SS	MS	F
Total	31	68,505.87	--------	
Subjects	7	15,720.37	--------	
Tests	3	16,579.62	5,526.54	2.30
Error	21	50,353.01	2,397.76	

Table A-2

Analysis of Variance for IL

Source	df	SS	MS	F
Total	31	868,843.5	---------	
Subjects	7	231,754.5	---------	
Tests	3	114,010.75	38,003.58	1.53
Error	21	523,078.25	24,908.49	

Table A-3

Analysis of Variance for EF

Source	df	SS	MS	F
Total	31	76.72	2.47	
Subjects	7	32.47	4.64	
Tests	3	5.35	1.78	0.96
Error	21	38.9	1.85	

Table A-4

Analysis of Variance for MF

Source	df	SS	MS	F
Total	95	1,587.63		
Subjects	7	386.96		
Tests	3	50.88	16.96	1.45
Tests x Subjects	21	245.79	11.70	
Series	2	40.75	20.37	1.42
Tests x Series	6	62.25	10.38	0.73
Error	56	801.00	14.30	

Table A-5

Analysis of Variance for IF

Source	df	SS	MS	F
Total	95	578.24		
Subjects	7	65.82		
Tests	3	9.28	3.09	1.32
Tests x Subjects	21	49.14	2.34	
Series	2	298.08	149.04	58.4 *
Tests x Series	6	13.26	2.21	0.87
Error	56	142.66	2.55	

* $p < .001$

Table A-6

Analysis of Variance for EL

Source	df	SS	MS	F
Total	95	5,052,443.62		
Subjects	7	769,691.78		
Tests	3	16,472.87	5,490.96	0.19
Tests x Subjects	21	603,618.30	28,743.73	
Series	2	1,836,230.81	918,115.40	30.08 *
Tests x Series	6	116,828.69	19,471.45	0.64
Error	56	1,709,601.17	30,528.59	

* $p < .001$

Table A-7

Analysis of Variance for MIII

Source	df	SS	MS	F
Total	95	164,176.34	--------	
Subjects	7	59,810.29	--------	
Tests	3	852.76	284.25	0.21
Tests x Subjects	21	28,924.62	1,377.36	----
Series	2	5,606.91	2,803.45	2.46
Tests x Series	6	5,204.93	867.49	0.76
Error	56	63,776.83	1,138.87	----

Table A-8

Analysis of Variance for PEI

Source	df	SS	MS	F
Total	95	624,997.74		
Subjects	7	345,070.66		
Tests	3	15,956.44	5,318.81	1.81
Tests x Subjects	21	61,753.3	2,940.63	
Series	2	138,707.14	69,353.57	68.42 *
Tests x Series	6	6,743.03	1,123.84	1.11
Error	56	56,767.17	1,013.70	

* $p < .001$

APPENDIX B

ANALYSES OF VARIANCE FOR EXPERIMENT 2

Table B-1

Analysis of Variance Comparing Estrus Condition for ML

Source	df	SS	MS	F
Between	1	32,587.74	32,587.74	2.15
Within	26	392,798.69	15,107.64	

Table B-2

Analysis of Variance Comparing Estrus Condition for IL

Source	df	SS	MS	F
Between	1	268,884.00	268,884.00	4.52 *
Within	26	1,546,616.85	59,485.26	

* $p < .05$

Table B-3

Analysis of Variance Comparing Estrus Condition for EF

Source	df	SS	MS	F
Between	1	7.03	7.03	2.42
Within	26	75.60	2.91	

Table B-4

Analysis of Variance Comparing Estrus Condition for MF

Source	df	SS	MS	F
Total	55	992.84		
Between	27	761.34		
Condition	1	11.0	11.0	0.38
Error	26	750.34	28.86	
Within	29	231.50		
Series	1	80.16	80.16	15.07 *
Series x Condition	1	7.71	7.71	1.45
Error	27	143.63	5.32	

*
$p < .001$

Table B-5

Analysis of Variance Comparing Estrus Condition for IF

Source	df	SS	MS	F	
Total	55	915.55			
Between	27	208.05			
Condition	1	48.75	48.75	7.96	*
Error	26	159.3	6.12		
Within	29	707.5			
Series	1	522.16	522.16	101.58	**
Series x Condition	1	46.61	46.61	9.07	*
Error	27	138.73	5.14		

* $p < .01$

** $p < .001$

Table B-6

Analysis of Variance Comparing Estrus Condition for EL

Source	df	SS	MS	F
Total	55	355,263,033.1		
Between	27	1,563,098.63		
Condition	1	11,901.17	11,901.17	0.19
Error	26	1,551,197.46	59,661.44	
Within	29	353,699,934,40		
Series	1	3,336,456.37	3,336,456.37	0.26
Series x Condition	1	50,856.79	50,856.79	0.003
Error	27	350,312,621.20	12,974,541.53	

Table B-7

Analysis of Variance Comparing Estrus Condition for MIII

Source	df	SS	MS	F
Total	55	88,271.0		
Between	27	51,962.87		
Condition	1	6,111.77	6,111.77	3.25
Error	26	48,851.1	1,878.88	
Within	29	36,308.13		
Series	1	5,468.77	5,468.77	5.15 *
Series x Condition	1	2,166.49	2,166.49	2.04
Error	27	28,672.87	1,061.98	

* $p < .05$

Table B-8

Analysis of Variance Comparing Estrus Condition for PEI

Source	df	SS	MS	F
Total	55	300,652.13		
Between	27	254,395.13		
Condition	1	729.17	729.17	0.07
Error	26	253,665.96	9,756.38	
Within	29	46,257.0		
Series	1	2,958.02	2,958.02	1.85
Series x Condition	1	150.47	150.47	0.09
Error	27	43,148.51	1,598.09	

BIOGRAPHICAL SKETCH

Daniel Quen Estep was born March 19, 1949 in San Antonio, Texas. In May, 1967 he graduated from Robert E. Lee High School in Baytown, Texas and in the fall of 1967 enrolled in the University of Texas at Austin. He graduated from the University of Texas at Austin in May, 1971, receiving a Bachelor of Arts degree with a major in Psychology. In September, 1971 he enrolled in the Department of Psychology of the Graduate School of the University of Florida.

In December, 1973 he received a Master of Arts degree in psychology from the University of Florida. Since January, 1974 he has been working towards the Doctor of Philosophy degree under the direction of Professor Donald A. Dewsbury.

Daniel Quen Estep is married to the former Barbara Melton of Dallas, Texas.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Donald A. Dewsbury, Chairman
Professor of Psychology

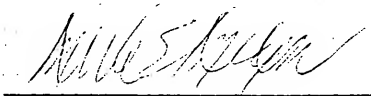
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

J. H. Kaufmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

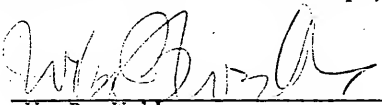
E. F. Malagodi
Associate Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



M. E. Meyer
Professor of Psychology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1975.

Dean, Graduate School